COLDWATER LAKE AND RESERVOIR RESEARCH

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The results of the research investigations contained in this report represent work of the authors and may or may not have been implemented as Parks and Wildlife policy by the Director or the Wildlife Commission.

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COLDWATER LAKE AND RESERVOIR RESEARCH

Period covered: May 2018 – November 2020.

RESEARCH GOALS:	Address questions and problems facing lake and reservoir fisheries managers throughout Colorado. Use field sampling, modeling and experiments to (1) diagnose the primary factors (e.g., harvest, habitat, recruitment, food supply, competition, predation or disease) driving the dynamics or limiting the production of important populations of fish; (2) use this information to identify and evaluate alternative approaches for improving or maintaining fish populations and their fisheries; and (3) develop new standardized sampling tools and reference points that improve the robustness of monitoring data and enable rapid assessment of fishery condition.

RESEARCH PRIORITY:	Summer Profundal Index Netting for monitoring Lake Trout.

OBJECTIVES:

Use standard survey methods to estimate the abundance and size structure of Lake Trout in key coldwater reservoirs.

INTRODUCTION:

Lake Trout are top predators, reproduce naturally, and are important sport and food fish for anglers in Colorado's lakes and reservoirs. Monitoring their abundance and size structure is necessary for assessing the appropriateness of harvest regulations, ensuring Lake Trout remain in balance with prey fish populations, and determining whether management goals are achieved. However, estimating the abundance of Lake Trout in large coldwater reservoirs at the frequency needed to inform management using conventional methods such as mark-recapture is impractical.

Summer Profundal Index Netting (SPIN) is a quantitative survey method for rapidly estimating the density of Lake Trout (Sandstrom and Lester 2009). Previous investigations by Colorado Parks and Wildlife concluded that SPIN is a viable alternative to more intensive methods for estimating and tracking trends in the abundance of Lake Trout to help guide management (Lepak 2011; Lepak 2013). Four water bodies have been sampled using SPIN: Taylor Park Reservoir (surveyed in 2013), Lake Granby (2014), Grand Lake (2013, 2016), and Blue Mesa Reservoir (2011, 2014, 2016, 2018, and 2020). Results from the 2018 and 2020 surveys on Blue Mesa Reservoir are reported here.

METHODS:

SPIN uses suites of standardized gill nets (three 1.8×64 m nets consisting of eight panels with mesh sizes of 57-, 64-, 70-, 76-, 89-, 102-, 114- and 127-mm stretch measure placed in random order) to capture Lake Trout in a way that allows us to estimate the density of Lake Trout directly (i.e., number per ha). These estimates of density are then scaled up to a total abundance based on the area of the lake or reservoir surveyed.

Catch rates of Lake Trout in gill nets fished in Colorado reservoirs are compared to catch rates of Lake Trout in the same type of gill nets in other water bodies where independent estimates of Lake Trout density were available. The catch is adjusted for the size-selectivity of the gill nets. Nets are set along the bottom in random orientation. Set locations are selected at random and stratified by depth (2-10 m, 10-20 m, 20-30 m, 30-40 m, 40-60 m, 60-80 m, and >80 m). Sampling is also stratified by different regions within the lake or reservoir if necessary, to account for differences in Lake Trout habitat. Sampling is conducted when surface temperatures exceed 18°C and the nets are set for two hours during daylight. Netting was conducted from 9 to 12 July, 2018 and from 10 to 14 August, 2020 in Blue Mesa Reservoir. The power of this method is the use of data from numerous other systems as a calibration tool to quantify Lake Trout densities in Colorado that can be used to estimate total abundance versus techniques that just provide estimates of relative abundance through time and across systems.

RESULTS & **DISCUSSION**:

Sampling was completed over the course of four days during 2018, wherein 95 nets were set capturing a total of 313 Lake Trout ranging in size from 210 mm to 862 mm FL (mean = 374 mm ± 88 mm SD). Sampling was completed over the course of four days during 2020, wherein 90 nets were set capturing a total of 212 Lake Trout ranging in size from 267 mm to 743 mm FL (mean = 401 mm ± 94 mm SD). Lake Trout were most prevalent in 20-30 and 30-40 m depths across Iola, Cebolla, and Sapinero basins in both years.

The depth distribution, size structure and extent of the catch in 2018 and 2020 at the corresponding water surface elevations of the reservoir produced a total Lake Trout abundance estimate of 29,857 fish ≥210 mm FL (lower 68% confidence limit = 23,826; upper limit = 36,702) and 16,443 fish ≥267 mm FL (lower 68% confidence limit = 12,518; upper limit = 20,842), respectively. The catch of Lake Trout <250 mm FL was incidental (0.32% of catch in 2018 and 0.00% in 2020). Therefore, these abundance estimates best reflect those of fish ≥250 mm FL as in previous SPIN surveys on Blue Mesa Reservoir (Sandstrom and Lester 2009; Table 1).

We examined whether there has been a disproportionate change in the estimated abundance of Lake Trout ≥363 mm FL or 400 mm TL (predominately age 4 and older) when compared to all fish vulnerable to the gear in Blue Mesa Reservoir over the period of record. In general, this length cutoff encompasses the most piscivorous fraction of the Lake Trout population, and those most vulnerable to anglers and ongoing suppression efforts (Lepak 2011; Pate et al. 2014). Abundance estimates for this separate size group of fish were lower, but exhibited a similar declining temporal trend as those incorporating all sizes of Lake Trout between 2011 and 2016. This indicated that

there was not a disproportionate change in the abundance of this secondary size group when compared to all sizes of fish over the 2011-2016 period (Figure 1). However, this pattern changed in 2018 whereby the abundance of Lake Trout ≥400 mm TL continued to decline while the estimated abundance of all fish vulnerable increased (Figure 1). This indicated that there was a pulse of small fish that were not yet fully vulnerable to capture by anglers or suppression efforts about to enter the piscivorous size range.

Table 1. Summary data from each SPIN survey conducted to date. Abundance estimates are for all Lake Trout vulnerable to the sampling gear (generally those ≥250 mm FL or 275 mm TL). The acronym LCL stands for lower 68% confidence limit, and UCL stands for upper 68% confidence limit for the abundance estimate. Adjusted CUE is the area-weighted (area of different depth strata and reservoir basins) catch of Lake Trout per gill net set, after also correcting the catch for size-selectivity. Asterisks indicate the presence of *Mysis diluviana*.

Survey year	Lake or reservoir	Number of net sets	Number of lake trout caught	Mean total length (mm)	SD of total length (mm)	Adjusted CUE	Density (fish/ha)	Total area surveyed (ha)	Abundance estimate	LCL	UCL
2011											
	Blue Mesa	81	129	437	110	2.29	11.14	3,059	34,071	27,144	41,929
2013											
	Grand Lake*	36	87	419	107	2.61	12.71	193	2,452	1,974	2,996
	Taylor Park*	36	271	416	94	4.03	19.61	610	11,950	9,871	14,341
2014											
	Blue Mesa	81	211	425	97	1.61	7.85	3,409	26,753	18,383	33,716
	[a]Lake Granby*	71	501	417	79	11.78	57.26	2,780	159,193	135,533	186,844
2016											
	Blue Mesa	83	180	438	114	1.47	7.15	3,409	24,368	16,538	30,948
	Grand Lake*	36	109	436	147	3.34	16.22	193	3,131	2,561	3,783
2018											
	Blue Mesa	95	313	414	98	2.34	11.36	2,629	29,857	23,826	36,702
2020											
	Blue Mesa	90	212	441	92	1.51	7.32	2,247	16,443	12,518	20,842

[a]Estimates for Lake Granby are subject to change. Food web interactions could make Lake Trout more vulnerable to the sampling gear causing the SPIN method to overestimate their abundance.

Comparing the size structure of Lake Trout captured during the 2018 SPIN survey to previous years confirmed that there was a higher frequency of small fish <400 mm TL (predominately age 2-3; Pate et al. 2014) present in the system, and that these fish would grow into a more piscivorous size range within the next 1-2 years (Figure 2). In addition to being ecologically significant, we detected a statistically significant difference in the size structure of Lake Trout captured during SPIN in 2011, 2014, 2016, and 2018 (Kruskal-Wallis One Way Analysis of Variance on Ranks; $H = 70.76$; $P < 0.001$) (Figure 3). Post-hoc comparisons to determine which years differed from each other indicated that the size structure of Lake Trout captured in 2018 differed from those captured in 2014 and 2016 ($P < 0.005$), largely due to the greater frequency of fish <400 mm TL (Figure 2). Because this pulse of small fish was likely comprised of age 2-3 individuals, it seems reservoir conditions during the 2014-2015 spawning seasons for Lake Trout were favorable.

Given the reduced abundance of piscivorous-sized Lake Trout as estimated from SPIN and corresponding boosts in the abundance of kokanee, fall suppression netting was not completed in

2018 or 2019. Rather, an incentivized angler harvest tournament for Lake Trout ≤660 mm TL was conducted winter through early summer in 2020 in anticipation for the pulse of small fish observed in 2018 entering the size range fully vulnerable to anglers. Thus, the 2020 SPIN survey was completed after the tournament was concluded and reflects angler harvest that accrued earlier in the year. Tournament anglers turned in 4,055 Lake Trout, 44% (1,791) of which were fish ≥400 mm TL. The smallest fish turned in was 203 mm TL. Relative to 2018, the estimated abundance of all fish vulnerable in 2020 was much reduced, whereas the estimated abundance of piscivorous-sized fish was slightly elevated supporting the notion that small fish observed in 2018 recruited into the piscivorous size range as anticipated (Figure 1). The higher relative frequency of fish ≥400 mm observed in the SPIN catch in 2020 compared to 2018 also supported this notion (Figure 2). Overall, SPIN data suggested that angler harvest and natural mortality that accumulated between summers 2018 and 2020 were sufficient to reduce total Lake Trout numbers and keep piscivorous-sized fish near their relatively low 2018 levels.
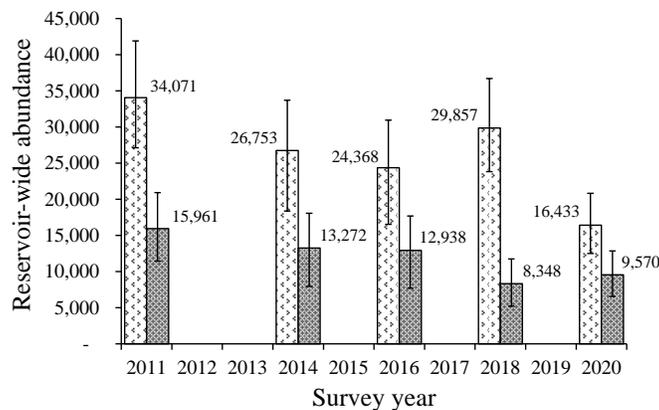
Figure 1. Abundance estimates for all Lake Trout vulnerable to the sampling gear (generally those ≥250 mm FL or 275 mm TL) in Blue Mesa Reservoir (white bars) and just those ≥363 mm FL or 400 mm TL (gray bars) from all SPIN surveys conducted to date. Error bars represent 68% confidence intervals.
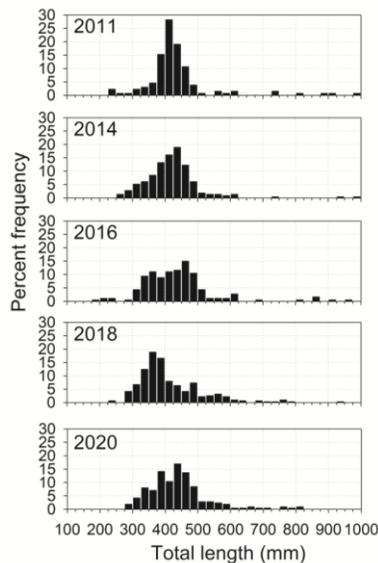
Figure 2. Length-frequency distributions (25 mm size bins) of Lake Trout captured during consecutive SPIN surveys on Blue Mesa Reservoir.

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RESEARCH PRIORITY: Population reconstruction and assessment of Lake Trout in Blue Mesa Reservoir to help inform new angler harvest incentive program.

OBJECTIVES:

Synthesize existing survey data from Blue Mesa Reservoir to estimate (1) the historic population trajectory of Lake Trout, (2) the productivity of Lake Trout and variation in recruitment, (3) total angler harvest over time, and (4) contemporary angler harvest rates. Use this information to predict future Lake Trout population trajectories and corresponding uncertainty based on harvest levels observed during the new angler incentive program and assess whether these levels are sufficient to maintain coexistence with kokanee and trophy Lake Trout without fall suppression netting.

INTRODUCTION:

Predation from naturally reproducing Lake Trout in Blue Mesa Reservoir (BMR) can become unsustainable and lead to rapid declines in kokanee and reduced growth and body condition of Lake Trout. Excessive predation on kokanee by an expanding population of Lake Trout put both fisheries at risk during the 1990's and 2000's despite the progressive relaxation of harvest regulations on Lake Trout and exhausting hatchery rearing space by doubling the annual stocking of kokanee fry (Johnson and Martinez 2000; Martinez et al. 2009). However, continued research and management including fall suppression netting for small Lake Trout initiated in 2009 combined with favorable reservoir conditions led to notable boosts in kokanee abundance and Lake Trout condition recently (Pate et al. 2014; Hansen 2018; Brauch 2019).

Given the dynamic interactions among kokanee, Lake Trout and anglers, management of the BMR fishery must remain adaptive. The combination of hydroacoustics (conducted annually) and SPIN (conducted every other year) enables rapid assessment of kokanee and Lake Trout and adjustment of management actions if deemed necessary. However, we still lack the quantitative tools that (1) effectively integrate these different types of standardized survey information, (2) account for uncertainty in survey estimates and other vital rates governing population dynamics, and (3) enable reliable prediction of population responses to management actions over a time-frame relevant to decision making and in a way that accounts for key uncertainties.

Previous age-structured models were useful for identifying how many and which age-classes of Lake Trout should be culled or transported annually during autumn gill-netting to optimize the tradeoff between kokanee egg production and the number of trophy-sized Lake Trout (Pate et al. 2014; Hansen 2016). However, these models required large amounts of data, do not readily accept routine survey data, do not consider annual variation in Lake Trout recruitment or angler harvest rate in their predictions, and were best suited for characterizing long-term equilibrium conditions.

Having a diverse suite of tools available to inform the short- and long-term dynamics of complex recreational fisheries should strengthen adaptive management programs. The goal of this study was to develop a new non-age-based population model for Lake Trout in BMR that complements existing age-structured models by (1) using the existing time-series of standardized survey

information (hydroacoustics, SPIN and angler creel) to estimate the parameters of and calibrate the new model to empirical data thereby making predictions of Lake Trout abundance and potential responses in kokanee more directly comparable to results from our routine monitoring surveys, and (2) using observation error from different survey estimates and the model fitting process to characterize uncertainty in key vital rates governing the population dynamics of Lake Trout.

METHODS:

Blue Mesa Reservoir has been studied and monitored extensively. As a result, it is one of Colorado's most data rich fisheries. Although fragmented, the time-series of survey data from angler creel (fishing effort, catch and harvest; 1989-2012), mark-recapture- (2002; Crockett et al. 2006) and SPIN-based estimates (2011, 2014, 2016, 2018) of Lake Trout abundance (predominately fish of catchable or predatory size), and numbers removed during fall suppression netting (2009-2017) contain complimentary information on how the population of Lake Trout vulnerable to anglers has changed through time and their productivity.

I used a Bayesian logistic growth model to predict the yearly (t) abundance (N), catch (C) and harvest (H) of catchable- ($\geq$12 inches) and predatory-sized ($\geq$17 inches) Lake Trout over the 1996-2012 period when independent estimates of abundance were available in two years (2002 and 2011) and of angler catch and harvest from creel surveys in all years (creel ceased in 2013). Comparing model predictions to survey estimates and their corresponding observation error allowed estimation of each size-groups maximum intrinsic rate of population change (r; Quinn and Deriso 1999), carrying capacity (K), and corresponding uncertainty in these parameters:

$$N_0 = N_{1996},$$
$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right) - H_t - R_t,$$

where R_t represents the number of Lake Trout removed during fall suppression netting. The result of model fitting is a distribution of plausible values (i.e., the 'posterior' distribution) for key parameters (r and K) that can be used for simulating future population trajectories and gauge how resilient Lake Trout are to angler harvest. The r of a population relates directly to their maximum per-capita recruitment rate (i.e., α in Ricker stock-recruitment model; Meyers et al. 1997), so in essence, represents an integrative measure of mean Lake Trout recruitment and variation therein to catchable or predatory size in the context of this analysis. The starting abundance of Lake Trout (N_0) was unknown, so treated as a fitted parameter in the model. I set $N_0 = N_{1996}$ to minimize potential influence from juvenile Lake Trout stocking events that occurred in 1989 and 1992.

Prior distributions on the parameters were non-informative: $r \sim$ U(-1.0; 1.0), $K \sim$ U(20,000; 80,000), and N1996 $\sim$ U(100; 10,000). I did not place an informative prior on r because existing information was sparse and only available for nonnative populations occupying large natural lakes containing invasive *Mysis diluviana* (e.g., Hansen et al. 2008) rather than a fluctuating reservoir with no *Mysis* and extensive stocking of kokanee and trout. However, the Bayesian approach offered an efficient method for integrating multiple sources of data, characterizing uncertainty, and ensuring model convergence.

To fit the logistic model to all survey data simultaneously (abundance, catch and harvest) and take advantage of the information that each contained for characterizing r and K, I assumed the creel-based values for annual fishing effort (E; total hours) were estimated with minimal error and incorporated two additional biologically relevant 'nuisance' parameters (Walters and Ludwig 1994) that effectively linked E and Lake Trout abundance to angler catch (the catchability coefficient q) and then angler catch to resulting harvest (the angler retention rate h):

$$C_t = qEN_t,$$

$$H_t = hC_t.$$

Creel-based estimates of E were consistently the most precise and slight deviations in E had minimal influence on posterior distributions for key parameters during preliminary model exploration. However, initial analyses indicated that q was lower during the 'standard' creel survey period (May through October; completed every year) than the winter ice-fishing period (January through April; completed in 2004, 2006 and 2012), so q was specific to each. Surprisingly, retention rate did not vary between periods, so only a single h was included. Although winter creel surveys were only conducted in three years, this was enough information to help recreate potential winter harvest over the full time-series and ultimately estimate total year-round harvest.

Once posterior distributions for r and K were characterized over the 1996-2012 period when independent estimates of harvest were available (r confounded otherwise), I then used these as informative priors and refit the logistic model to the time-series of SPIN estimates over the 2013-2018 period when creel information was unavailable to estimate the contemporary angler harvest rate (u):

$$N_0 = N_{2013},$$
$$N_{t+1} = N_t + rN_t\left(1 - \frac{N_t}{K}\right) - uN_t - R_t.$$

The prior for N_{2013} followed a normal distribution with mean and standard deviation calculated from the set of model predicted abundances at the start of that year generated from the first phase of model fitting above. Similarly, the prior for u followed a normal distribution with mean and standard deviation calculated from the corresponding set of model predicted harvest rates in 2012.

I obtained posterior distributions of the parameters using Markov-Chain-Monte Carlo (MCMC) methods following the Metropolis-Hastings algorithm (Gelman et al. 1997) coded in R. An MCMC chain is a random walk through parameter space whereby successive, correlated sets of parameter values are chosen ('draws') and judged based on criteria that ultimately allows the chain to converge on the joint posterior distributions. I ran one MCMC chain of length 10 million, discarded the first 20% ('burn-in' period), and subsampled 10,000 draws at regular intervals to remove autocorrelation. Starting parameter values were varied to ensure convergence. Lastly, I assumed that all survey estimates followed a lognormal distribution with standard deviation approximated by their corresponding coefficient of variation (CV) when computing the negative log-likelihood

of each survey data point given the proposed parameters within the MCMC chain. The overall modeling approach described here followed the guidance and theoretical approach of Hilborn and Mangel (1997) and Branch et al. (2004).

RESULTS & DISCUSSION:

Integrating over all survey data and reconstructing the historic population trajectory of Lake Trout in BMR (Figure 1) revealed new insights that should help management of the fishery and garner public support for an angler harvest incentive program and the continued suppression of small fish.
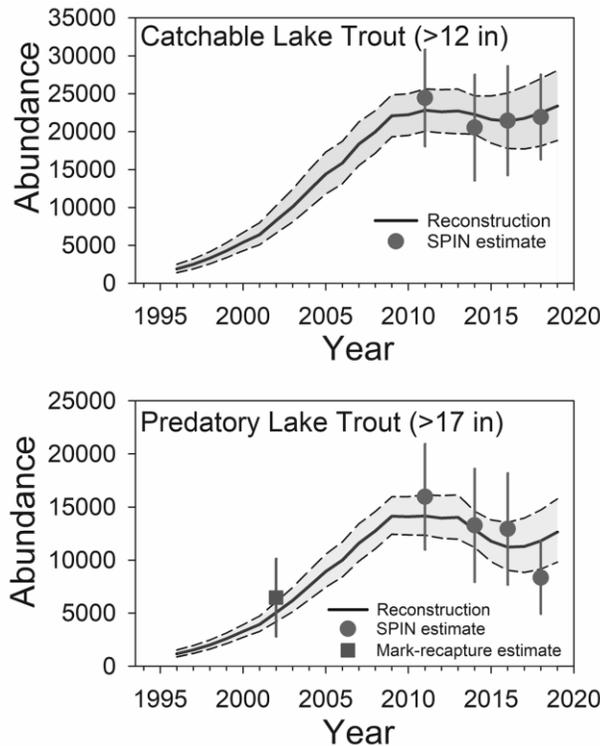
Figure 1. Reconstructed population trajectories generated from a Bayesian logistic growth model for catchable- and predatory-sized Lake Trout in Blue Mesa Reservoir. Shaded regions represent 95% credible intervals. Points represent independent estimates of Lake Trout abundance from routine SPIN or intensive mark-recapture surveys. Error bars represent ± 1SE.

Overall, model results indicated that (1) the Lake Trout population expanded 3 to 5-fold since the 1990's, (2) the productivity of Lake Trout as represented by their estimated maximum intrinsic rate of population change (r) was relatively high, density-dependent, and comparable to nonnative populations fueled by invasive *Mysis diluviana* (see below), (3) added mortality from fall suppression netting combined with density-dependent reductions in productivity as the Lake Trout population expanded was ultimately sufficient to curtail growth (particularly for predatory-sized fish), and (4) Lake Trout are currently around half of their estimated carrying capacity. In addition, the model-based estimates of total numbers harvested by anglers (Figure 2) and corresponding harvest rates (including fall removals) rarely approached those considered unsustainable (≥50% annually) for Lake Trout in their native range (Healy 1978; Shuter et al. 1998) and were exhibiting a declining trend before fall suppression netting started in 2009 (Figure 3).

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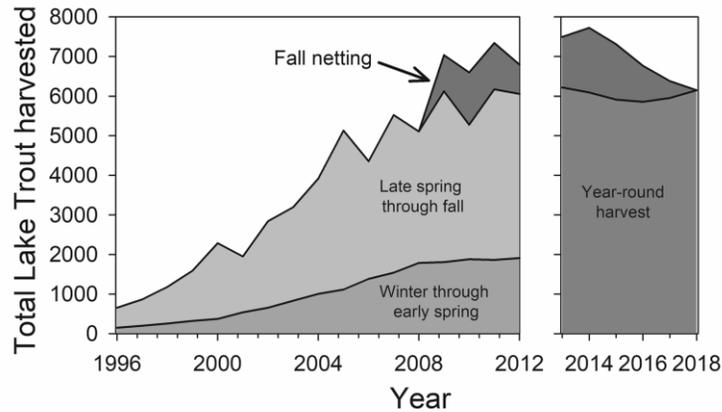
Figure 2. Model-based estimates for the total number of Lake Trout harvested over time by anglers in relation to numbers removed during fall suppression netting. Note that ~50% of angler harvest was comprised of piscivorous-sized Lake Trout, but ~98% for fall suppression netting.

Collectively, these results provide evidence that the open-access (i.e., fishing effort not regulated) Lake Trout fishery in BMR has been sustainable and resilient to overharvest over its intensively monitored history. The population has supported relatively high levels of recreational harvest on small Lake Trout annually, which is needed to meet fisheries objectives related to maintaining coexistence with plentiful kokanee and trophy potential in larger, older Lake Trout (Pate et al. 2014). For the remainder, I use key results from this analysis and general principles of the logistic growth model to demonstrate how incentivizing greater harvest of small fish could continue to enhance the fishery, why the Lake Trout population should remain resilient to elevated harvest, and how this information can be used to develop more refined management goals moving forward.
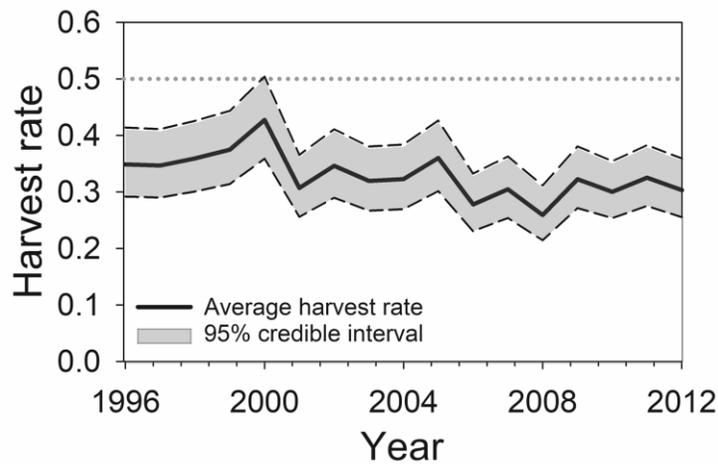
Figure 3. Model-based estimates of angler harvest rate of catchable-sized fish over the 1996-2012 period in relation to those considered unsustainable for Lake Trout in their native range (≥50% annually; Shuter et al. 1998).

First, the logistic growth model fit the survey data well (Figures 1 and 4). In addition, final posterior distributions for r and K were well defined, further supporting the appropriateness of the logistic model for characterizing the population dynamics of catchable- and predatory-sized Lake Trout (Figure 5). A key assumption of the logistic model is that productivity is density-dependent. Simpler models that excluded density-dependence did not fit the data well during preliminary

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analyses. Although underlying mechanisms cannot be clarified here, it appears density-dependent productivity is an important process governing the dynamics of Lake Trout in BMR which has implications for managing the fishery.
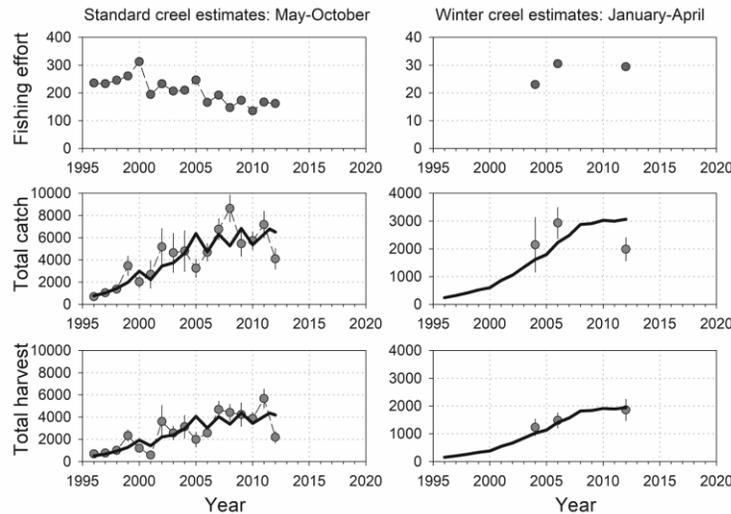
Figure 4. Time-series of fishing effort (1,000's of hours) and the total catch and harvest of catchable-sized Lake Trout in Blue Mesa Reservoir estimated from standard (left panels) or winter (right panels) angler creel surveys (points) over the 1996-2012 period. Error bars represent ± 1SE. Lines represent the fit of the Bayesian logistic growth model.
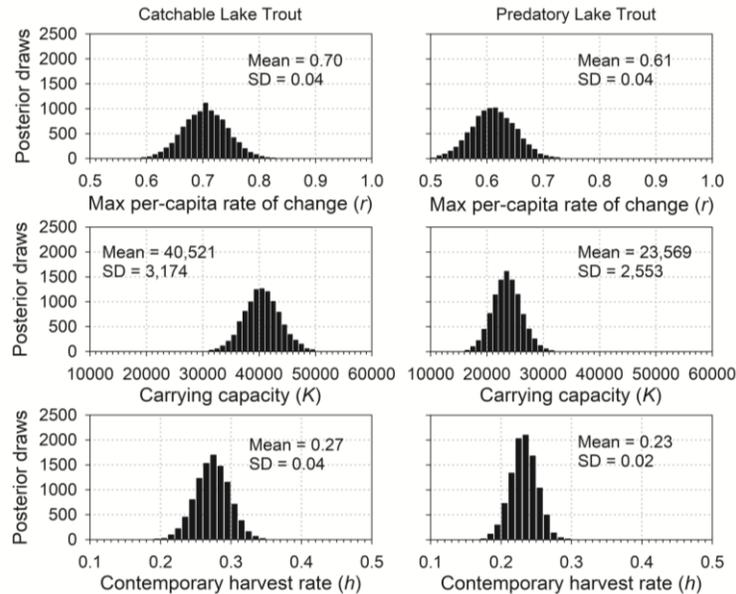
Figure 5. Final posterior distributions (frequency of 10,000 independent draws from MCMC chains) estimated for key parameters governing the population dynamics of catchable- (≥12 inches) and predatory-sized (≥17 inches) Lake Trout in Blue Mesa Reservoir based on survey data collected over the 1996-2012 period. The mean (μ) and standard deviation (σ) of each distribution is noted on each panel.

The logistic model incorporates density-dependent productivity by linearly reducing r toward zero as population size approaches K. Therefore, the r estimated for Lake Trout in BMR represents the maximum intrinsic rate of increase expected at very low abundance, not what would be anticipated

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across all population sizes (Figure 6). The posterior mean of r for predatory Lake Trout was 0.61. During the initial expansion of similar-sized Lake Trout in Lake Pend Orielle, Idaho, r was estimated at 0.63 (Hansen et al. 2008). So, the estimated maximum productivity of Lake Trout in BMR over 1996-2012 was comparable to an expanding *Mysis*-fueled population (Stafford et al. 2002; Hansen et al. 2007) and suggests that they could replace themselves relatively quickly at low abundance if harvest rates remained similar to historic or contemporary levels. The posterior mean of u estimated for predatory-sized Lake Trout over the 2013-2018 period was 0.23 (Figure 5), and historic rates were around 0.3—both fall well below the theoretical equilibrium threshold with r at low abundance levels (Figure 6).
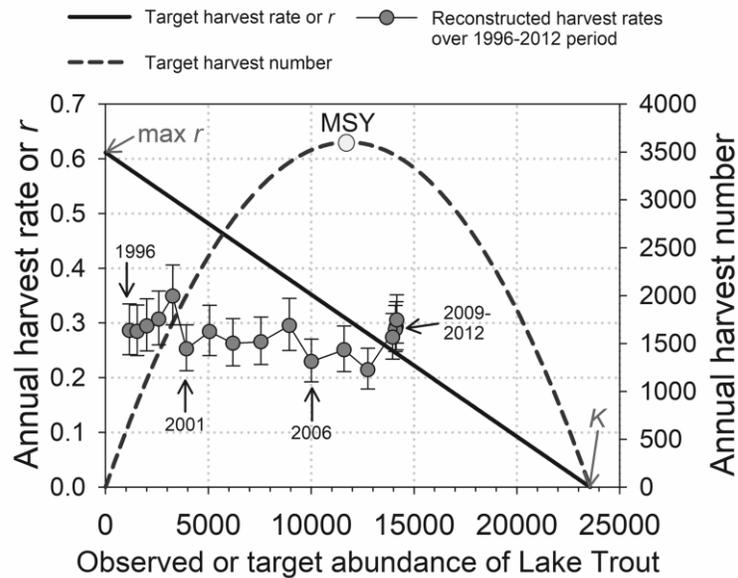
Figure 6. Theoretical relationships between the annual harvest rate (solid line) and the corresponding annual harvest number (dashed line) required to maintain a specific abundance of predatory-sized Lake Trout (x-axis) in Blue Mesa Reservoir assuming stable equilibrium conditions. The peak of the dashed line represents maximum sustainable yield (MSY). In addition to harvest rate, the solid line represents how the estimated maximum intrinsic rate of population change (max r) declines as the abundance of Lake Trout increases toward the estimated carrying capacity (K) of the population. Points represent the harvest rates achieved by anglers as estimated from the Bayesian logistic model over the 1996-2012 period (points for 2009-2012 include added harvest from fall suppression netting). Error bars are 95% credible intervals. The temporal progression of reconstructed harvest rates from left to right corresponds with the expanding population of Lake Trout. Thus, while harvest rates remained below r, the Lake Trout population continued to grow until boosts in harvest rate from fall suppression netting beginning in 2009 were sufficient to exceed the equilibrium threshold with r.

For exploited fish populations, high per-capita recruitment rates at low abundance guards them from overharvest, particularly when large, old, reproductive individuals are protected (Meyers and Mertz 1998; Hixon et al. 2014), or when anglers maintain catch-and-release of large fish despite relaxed regulations—common in trophy Lake Trout fisheries such as BMR (Martinez et al. 2009). For invasive populations, high per-capita recruitment rates make them difficult to suppress to pre-expansion levels once more established (Munro et al. 2005; Syslo et al. 2011), highlighting the importance of initiating suppression programs soon after detection (Dux et al. 2019). Depensation could increase risk of overharvest but this behavior is rare in exploited fish stocks (Hilborn et al. 2014) and Lake Trout can achieve near maximum recruitment levels when spawner abundance is

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reduced to 20% of unexploited levels (Meyers et al. 1999). In addition, an explicit goal of management at BMR is to maintain trophy potential in larger, older, fecund Lake Trout. The presence of these fish helps maintain productivity and stability in exploited populations (Hixon et al. 2014). Thus, concerns of overharvesting Lake Trout in BMR through angler incentives is unwarranted. Albeit variable, steady recruitment of Lake Trout into the piscivorous size range is more likely.

According to the logistic model, anglers would need to harvest at a progressively higher rate annually in order to suppress Lake Trout in BMR to a progressively lower target abundance level, then sustain an elevated harvest rate once that target is achieved. For example, to reduce the abundance of predatory-sized Lake Trout to levels observed during the early 2000's when predator-prey conditions were highly favorable for Lake Trout prior to kokanee collapse (Figure 7), contemporary angler harvest rates would need to increase two-fold or more (Figure 6). In an open-access recreational fishery such as BMR, this would require sufficient and sustained increases in fishing effort (E), catchability (q) and or retention (h) if relying on anglers alone. Incentivized angling was used to help suppress invasive Lake Trout in some large western lakes, but only successful when used in tandem with gill-netting (Hansen et al. 2016; Dux et al. 2019). Because BMR is small compared to these other natural lakes and complete suppression is not the goal, incentivized angling alone could be effective at maintaining coexistence between plentiful kokanee and trophy Lake Trout in the absence of fall suppression netting.
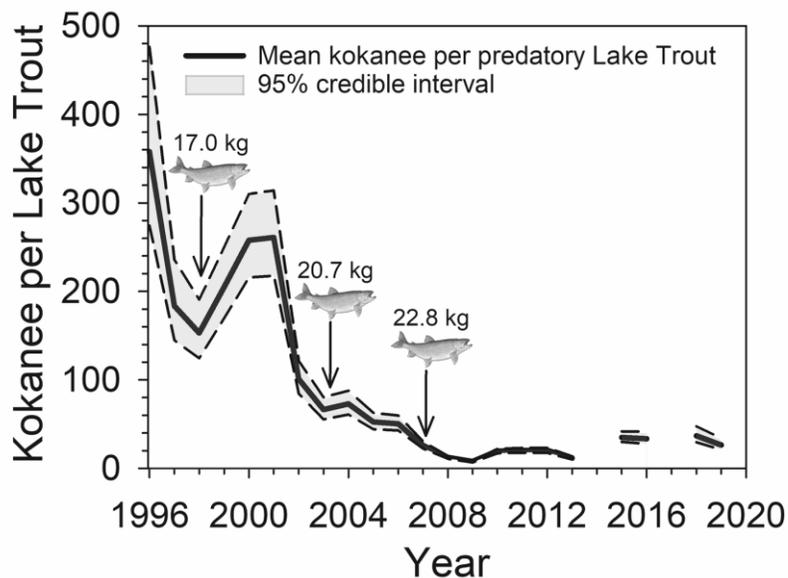
Figure 7. Predator-prey conditions in Blue Mesa Reservoir as represented by the ratio between the number of kokanee in the system estimated annually from standard hydroacoustics surveys and the number of predatory-sized Lake Trout reconstructed from the Bayesian logistic model. Arrows denote when record breaking fish were caught by anglers.

Reconstructing historic harvest rates achieved by BMR anglers when no incentives were present helped clarify the importance of fall suppression netting in curtailing continued expansion of Lake Trout. Harvest rates were exhibiting a declining trend prior to suppression and were not sufficient to keep pace with density-dependent reductions in r. Therefore, continued population expansion to over 15,000 predatory-sized Lake Trout (where angler harvest rate would have ultimately

converged with *r*) was likely. However, the initiation of suppression netting in 2009 boosted harvest enough to exceed the equilibrium threshold with *r* and halt growth more immediately (Figure 6). General principles of the logistic model and corresponding parameter estimates for Lake Trout in BMR can (1) provide useful reference points for evaluating the effectiveness of a new angler incentive program, (2) help develop informed management targets (e.g., annual harvest targets to achieve some desired abundance level), and (3) help frame discussions with the angling public.

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RESEARCH PRIORITY: Monitoring of gill lice and the distribution, size- and age-structure of kokanee in Blue Mesa Reservoir.

OBJECTIVES:

Characterize parasite-host dynamics between *Salmincola californiensis* and kokanee through intensive seasonal and annual monitoring of immature and mature fish in Blue Mesa Reservoir.

INTRODUCTION:

Pacific trout and salmon of the genus *Oncorhynchus* are susceptible to the freshwater ectoparasitic copepod *Salmincola californiensis*, also known as 'gill-lice' or 'gill-maggots' (*Salmincola* for remainder; Kabata 1969). Attachment points to host fish vary but include the gill filaments, branchial cavity, and fin rays (Kabata and Cousins 1977). Although low-level infections are not thought to cause mortality directly, anemia, reduced gas exchange and osmotic regulation, and poor swimming endurance are associated with severe infections (Pawaputanon 1980; Herron et al. 2018). These sub-lethal effects may contribute to higher mortality under stressful environmental conditions (Vaughan and Coble 1975; Hargis et al. 2014) or during critical life-stages such as smoltification and spawning (Herron et al. 2018; Barnett et al. 2020). High-prevalence (proportion of individuals parasitized) and intensity (number of adult parasites per fish) infections may impede recovery efforts for threatened species (Monzyk et al. 2015) and are implicated in the deterioration of some recreational fisheries (Vigil et al. 2016).

Infection prevalence and intensity depend on numerous interacting physical habitat, biological and species-specific factors. For example, parasite-host dynamics in some reservoir environments appear to amplify the infection of *Salmincola* when compared to streams, but more so for some species and life-stages than others. The infection prevalence, intensity and rate of accumulation for ages 0-1 Chinook Salmon *O. tshawytscha* occupying reservoirs of the Willamette River Basin, Oregon, exceeded those of conspecifics inhabiting adjacent streams both concurrently and historically pre-dam construction (Murphy et al. 2020). They also exceeded those of ages 0-1 kokanee (lacustrine Sockeye Salmon *O. nerka*), ages 0-3 Rainbow Trout *O. mykiss*, and larger bodied Cutthroat Trout *O. clarkii* sampled from the same reservoirs (Monzyk et al. 2015). Infections observed from Chinook Salmon reached levels that likely reduce the survival of outmigrating smolts by limiting gas exchange and osmotic regulation as inferred from diminished swimming endurance in both naturally and laboratory infected fish (Herron et al. 2018). The specific mechanisms leading to high-intensity infections for juvenile Chinook Salmon in Willamette reservoirs are uncertain, but suggest that *Salmincola* could be detrimental to other reservoir populations of ecologically or economically important trout and salmon.

Kokanee are an important sport, food and prey fish native or introduced to many North American lakes (Wydoski and Bennett 1981; Biser 1998). Kokanee and their anadromous counterpart interact with *Salmincola* within the native range of each species along the Pacific Rim (Kabata 1969; Bailey and Margolis 1987; Chigbu 2001). However, the distribution of *Salmincola* has expanded eastward through the movement and stocking of infected fish (Sutherland and Wittrock 1985; Kamerath et al. 2009; Ruiz et al. 2017) and now represents an emerging threat to some

introduced populations of kokanee supporting recreational fisheries in reservoirs where the parasite has not been present historically (Hargis et al. 2015). This is particularly true in Colorado. Declines in the abundance of mature kokanee concurrent with heavy *Salmincola* infestations were observed in Elevenmile, Cheesman and Clear Creek Reservoirs (Vigil et al. 2016). However, the progression and extent of these infestations in relation to environmental conditions or other factors that can influence the abundance or survival of kokanee (e.g., abundance of predators) were not well documented, leaving it difficult to discern the role of *Salmincola* in the population declines.

More recently, *Salmincola* was observed in Blue Mesa Reservoir, which supports Colorado's premier kokanee-Lake Trout fishery and is the primary source of kokanee eggs for supplying statewide stocking programs. The presence of *Salmincola* adds another layer of uncertainty to an already multifaceted fishery requiring complex management to maintain coexistence between hatchery-supported kokanee and naturally reproducing Lake Trout (Pate et al. 2014).

Therefore, we initiated and intensive monitoring program for tracking the seasonal and annual progression of *Salmincola* in relation to environmental conditions on both immature and mature kokanee at large in Blue Mesa Reservoir, and mature fish in the spawning run at Roaring Judy Hatchery (~20 miles upstream of reservoir) to better understand parasite-host dynamics and help address a number of basic questions. For example: (1) How does *Salmincola* infection vary seasonally and by kokanee age and maturity status? (2) Are juvenile kokanee accumulating adult *Salmincola* at a rate similar to juvenile Chinook Salmon in Willamette River Basin reservoirs wherein sub-lethal effects or mortality might be anticipated? (3) Do potential behavioral (e.g., pre-spawn aggregations) and physiological processes associated with the maturation process amplify accumulation more than expected by age alone prior to spawning? (4) Has *Salmincola* influenced the summer depth-distribution of kokanee to an extent that may require changes to standard hydroacoustics analyses? (5) Do *Salmincola* counts from mature kokanee during the spawning run at the Roaring Judy reflect conditions in the reservoir, or does congregating in hatchery ponds and raceways over a ~1-2 month period amplify intensity and prevalence, thereby skewing assessments of overall severity? (6) Is there evidence that the rate of *Salmincola* proliferation is slowing? Because this is an ongoing monitoring program, we may be able to ultimately identify potential critical thresholds for mortality and how kokanee density or other factors such as pelagic fish community composition regulate parasite loads in the reservoir.

METHODS:

Reservoir sampling.—Kokanee were sampled seasonally (spring, summer and fall) if possible from 2016-2020 in offshore waters of each basin of Blue Mesa Reservoir (Iola, Cebolla and Sapinero) using a standard suite of six multi-mesh vertical gill nets set overnight (Hansen 2019). The depth of each fish captured was recorded. Captured fish were also measured for total length (TL; mm), assessed for external signs of maturation, and then immediately placed in ice-water for additional processing in the laboratory. In the laboratory, TLs and weights (to nearest gram) were taken, sex and maturation was confirmed internally, and otoliths for age determination were extracted. Otoliths were aged through surface evaluation with a dissecting microscope (some aging has not yet been completed). A subset of otoliths were sectioned to confirm the surface-based ages. Visual counts of adult *Salmincola* by location on the fish (e.g., fins, gill filaments and buccal

cavity) were also noted (2018-2020 only). The ice-water holding the catch was filtered occasionally once laboratory processing was complete to assess whether any adult *Salmincola* were shed, but none were ever observed indicating this was an adequate method for preserving samples in the field prior to visual examination for adult *Salmincola*.

Hatchery sampling.—A random subsample of approximately 100 mature kokanee with an equal mix of males and females were collected weekly throughout the spawning run at Roaring Judy Hatchery over the 2016-2020 period. These fish were processed the same way as fish captured in vertical gill nets in the reservoir. The age of kokanee sampled each year from Roaring Judy were estimated from otolith mass rather than visually or through sectioning following the methods of Lepak et al. (2012).

RESULTS & DISCUSSION:

Reservoir catch and seasonal depth-distribution.—The catch of immature and mature kokanee in a standard suite of vertical gill nets fished overnight varied by season, basin and year (Figures 1-3). Catch was generally highest across years in Cebolla (Figure 2), particularly during summer thermal stratification. Pre-spawning aggregations of kokanee were most common in Cebolla during summer, but very few pre-spawning fish were encountered in summer 2020 when compared to previous years. Catch of kokanee in Sapinero (Figure 3) and Iola (Figure 1) were typically dominated by immature fish across all times of year.
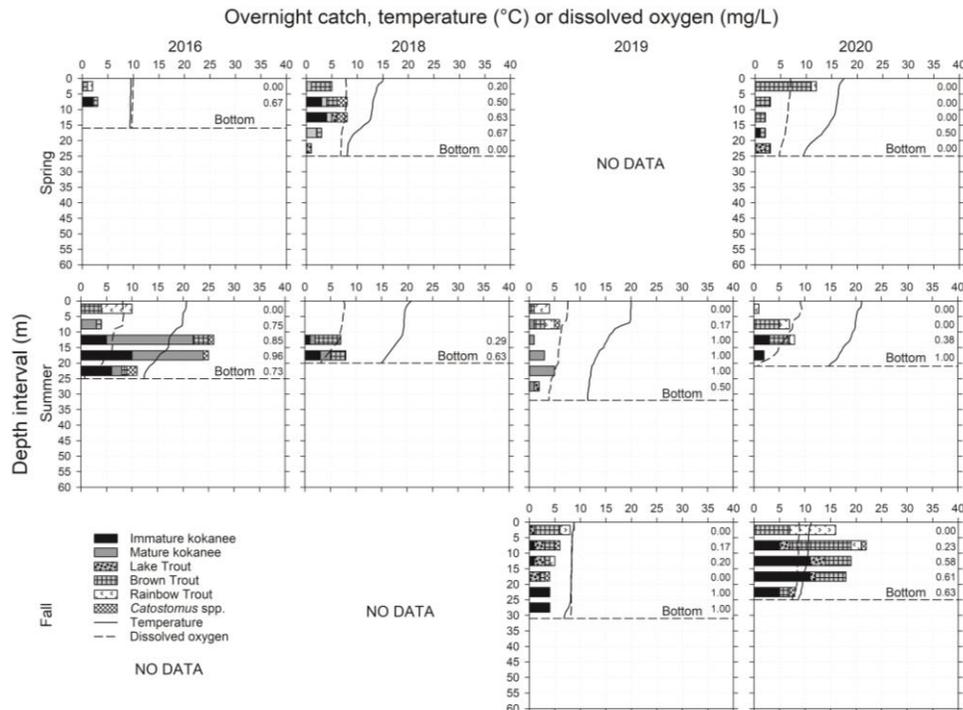
Figure 1. Seasonal and annual depth-specific vertical gill-net catch of kokanee and other fishes in Iola basin of Blue Mesa Reservoir over 2016-2020. Corresponding water temperature and dissolved oxygen conditions at the time of sampling are also presented. Summer surveys corresponded with concurrent standard hydroacoustics surveys for estimating the abundance of kokanee. Values represent the proportion kokanee captured in each 5 m depth strata.
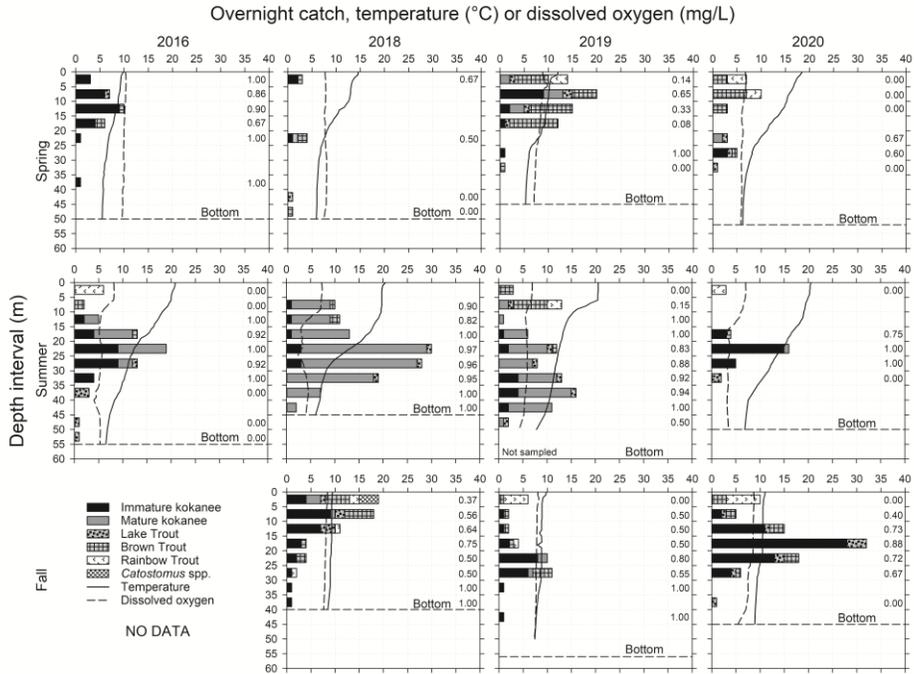
Figure 2. Seasonal and annual depth-specific vertical gill-net catch of kokanee and other fishes in Cebolla basin of Blue Mesa Reservoir over 2016-2020. Corresponding water temperature and dissolved oxygen conditions at the time of sampling are also presented. Summer surveys corresponded with concurrent standard hydroacoustics surveys for estimating the abundance of kokanee. Values represent the proportion kokanee captured in each 5 m depth strata.
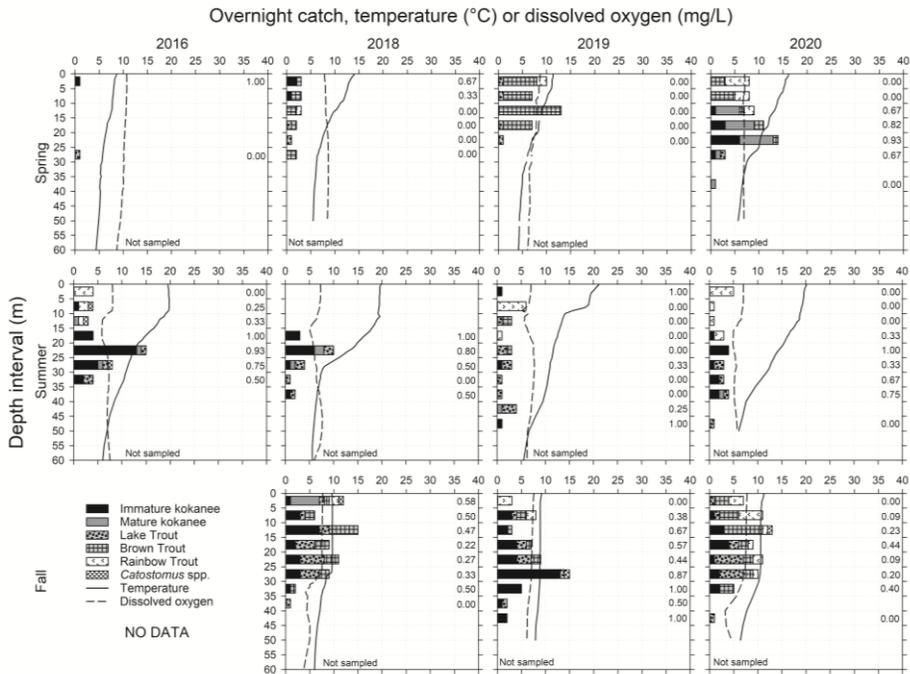
Figure 3. Seasonal and annual depth-specific vertical gill-net catch of kokanee and other fishes in Sapinero basin of Blue Mesa Reservoir over 2016-2020. Corresponding water temperature and dissolved oxygen conditions at the time of sampling are also presented. Summer surveys corresponded with concurrent standard hydroacoustics surveys for estimating the abundance of kokanee. Values represent the proportion kokanee captured in each 5 m depth strata.

A large number of pre-spawning kokanee were observed within shallow depths in Iola during summer 2016 when water temperatures were relatively warm (15-20°C) throughout the water column, which has not been observed to the same extent since. More recently, pre-spawning kokanee primarily congregated in deeper, cooler depths in Cebolla prior to up-river migration. This was particularly apparent in 2018 when reservoir surface elevations reached near record lows and Iola had diminished greatly, but a similar pattern was observed in 2019 when the reservoir refilled and surface elevations were higher than those in 2016—indicating that this shift in distribution was likely driven by factors other than fluctuations in water level and corresponding effects on vertical gradients in temperature and dissolved oxygen. Only two mature kokanee were captured across basins in 2020, which aligned with a poor adult return to Roaring Judy Hatchery. Despite low numbers of mature kokanee, a relatively large number of immature fish (ages 0-2) were captured across basins in November 2020, likely reflecting low entrainment or good survival or both.

Salmincola infection prevalence and intensity in reservoir fish.—Because otolith aging for some samples is not yet complete, I only report annual adult *Salmincola* prevalence and intensity for immature (primarily smaller and younger) versus mature (primarily larger and older) kokanee over the 2018-2020 period here. In addition, I've lumped counts across basins, seasons, sex and physical locations examined on each fish. However, future analyses will consider these different factors in addition to age as each likely contributes variation to the distributions of raw counts (Figure 4).
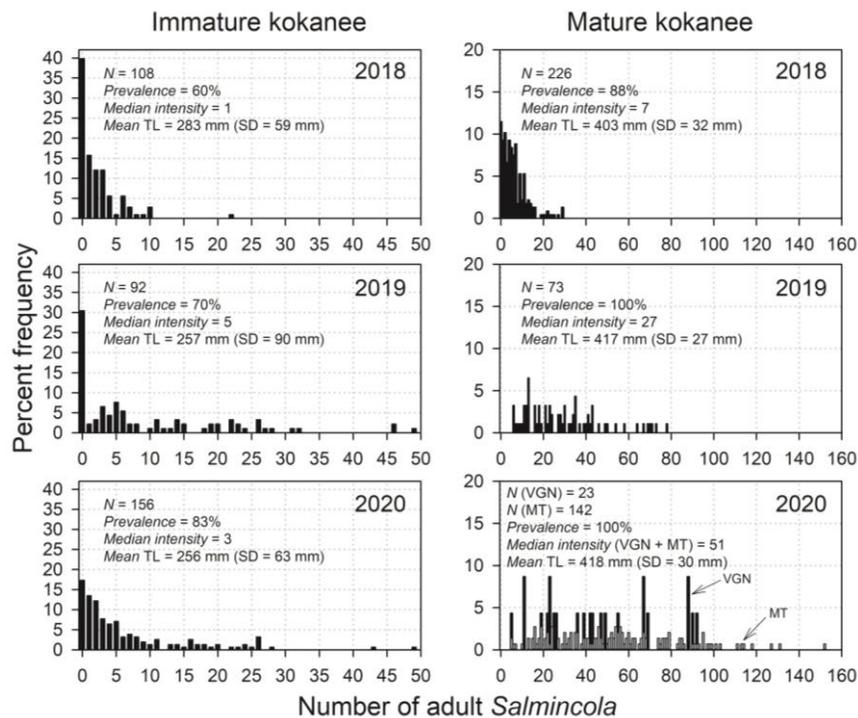
Figure 4. Count-frequencies of adult *Salmincola* on immature and mature kokanee sampled from Blue Mesa Reservoir over the 2018-2020 period. Counts were integrated across basins, seasons, sex and physical locations on each fish. Because vertical gill-net (VGN) catch of mature kokanee in 2020 was low (black bars), supplemental samples were taken from a Merwin trap (MT) fished through October in Cebolla basin (gray bars). The mean total length (TL; mm) and associated standard deviation (SD; mm) of kokanee sampled are provided. Note differences in axes between immature and mature fish.

Counts of adult *Salmincola* on kokanee were taken in the field during the summer vertical gill-netting survey in 2016. Prevalence was <5% and intensity was ≤2 adults per fish for immature and mature kokanee combined at that time (N = 137 fish examined). Since the onset of more intensive reservoir monitoring in 2018, infection prevalence has progressively increased for immature kokanee from 60% in 2018 to 83% in 2020. In addition, there was a large increase in intensity for immature fish between 2018 and 2019, but intensity remained the same between 2019 and 2020 (Figure 4). There was a significant difference in median infection intensity for immature fish among years (H = 33.56, df = 2, P <0.001; Kruskal-Wallis One Way ANOVA on Ranks). Post-hoc comparisons indicated that both 2019 and 2020 differed from 2018 (both P <0.001), but not from each other (P near 1.0).

Mature kokanee exhibited higher infection prevalence (now 100%) and intensity, but also much greater variation, than immature fish since the onset of intensive reservoir monitoring. Unlike immature fish, median intensity has progressively increased through time (Figure 4). There was a significant difference in median intensity for mature fish among years (H = 236.12, df = 2, P <0.001; Kruskal-Wallis One Way ANOVA on Ranks) and all year-by-year post-hoc comparisons were significant (all P <0.001). It is important to note that these analyses included fish sampled from the Merwin trap fished in Cebolla basin through October during 2020. However, the median intensity from mature fish captured in the Merwin trap alone did not differ from those captured in vertical gill nets earlier in the year (P = 0.64) so their inclusion was warranted.

Salmincola infection prevalence and intensity in the spawning run.—Similar to mature fish sampled seasonally in the reservoir, the prevalence and median intensity of adult *Salmincola* has progressively increased in the spawning run at Roaring Judy Hatchery over the 2016-2020 period (Figure 5). There was a significant difference in median infection intensity among years (H = 2,031.65, df = 4, P <0.001; Kruskal-Wallis One Way ANOVA on Ranks), and most pairwise comparisons between years were significant. However, despite some amplification, 2020 did not differ from 2019 (P = 0.07)—largely due to the highly variable count data with no strong mode (opposite from that observed in 2018) ranging from near zero to 100-120 adult *Salmincola* in both years. In addition, based on aging data from 2019 and 2020, the fish exhibiting relatively low infection intensities amidst growing parasite loads in the reservoir were still a mix of age-classes, not just the youngest individuals in the run (Figure 5). If this 'pancaking' effect on the distribution of adult *Salmincola* counts across the range of variation observed to date continues to persist, it could mean that (1) proliferation is slowing and or (2) some individuals are better able to resist/mediate the parasite (physiologically or behaviorally) than others and could be targeted for propagation at the hatchery. Logistically, this would require a spawning run of sufficient size (difficult if *Salmincola* grossly affects survival) and coarse sorting of males and females prior to spawning which would require a large team of volunteers.

These patterns could also be random and we still need to discern the role of kokanee density. The overall hydroacoustics-based estimates of kokanee abundance was stable over the 2016-2019 period (~400,000 fish; 2020 pending), but 2018 was nearly the lowest water level year on record which may have concentrated fish and contributed to the relatively large increase in median infection intensity observed in 2019 (Figure 5). Conversely, the reservoir was full in 2019 and spawner abundance appeared greatly reduced in 2020 based on catch in vertical gill nets. Both

factors could have tempered further exponential increases in infection intensity. Statistical models that can handle large variation in count data are currently being explored to evaluate the relative importance of different factors in driving adult *Salmincola* infection intensity.

In all years, the run was dominated by age 2 and age 3 kokanee, but the relative proportion of each varied year-to-year. Interestingly, no age 4 individuals were classified using the machine learning techniques developed by Lepak et al. (2012). During method development, predicting age from otolith mass and other covariates such as TL and sex using a random forests approach consistently under-estimated known age 4 individuals by one year of age and these fish are likely being missed in the current data set. In the future, we will need to use a hybrid approach and estimate age for the largest individuals sampled from the spawning run visually or through sectioning rather than from otolith mass to more adequately characterize the proportion of age 4 fish and their corresponding infection intensity.
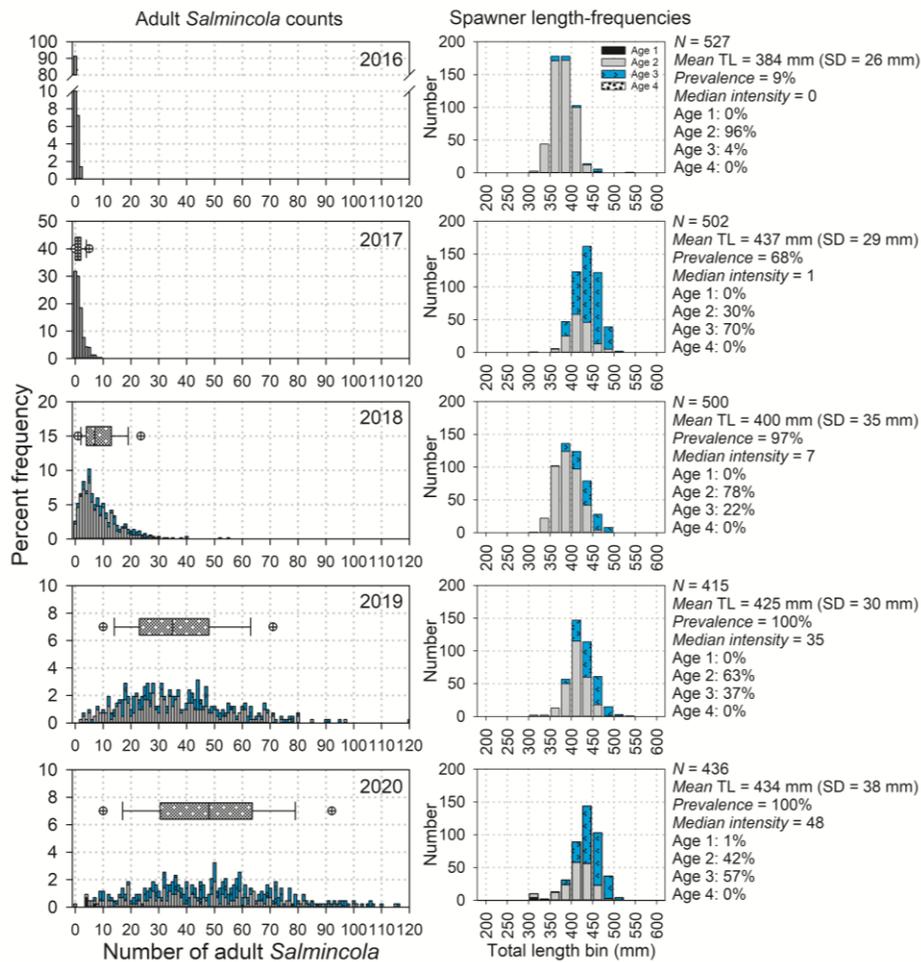
Figure 5. Percent frequency of adult *Salmincola* counts on mature kokanee returning to spawn at Roaring Judy Hatchery over the 2016-2020 period (left panels). For 2018-2020, count-frequencies were parsed among different age-classes of kokanee. Counts are also displayed as a box plot for 2017-2020 with the box representing the 25th, 50th (median) and 75th percentiles, whiskers representing the 10th and 90th percentiles, and the points representing the 5th and 95th percentiles. The corresponding length-frequencies of spawners (males and females combined) sampled each year are shown in the right panels. Length-frequencies were also parsed by age-class for 2016-2020.

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RESEARCH PRIORITY: Methods for correcting gill-net catch data for size-selective bias.

PUBLICATION:

Hansen, A. G. 2019. Size-dependent retention of pelagic-oriented kokanee in multimesh gill nets. North American Journal of Fisheries Management 39:921-932.

OBJECTIVES:

Develop tools for adjusting gill-net catch data for size-dependent retention probability so that minimally-biased estimates of size- and age-structure can be obtained for key species.

INTRODUCTION:

Multimesh gill nets are used extensively to sample fish in Colorado's coldwater reservoirs. Despite containing multiple panels of different sized mesh and generally catching a wide size-range of fish, these nets are still size-selective. This means that the rate at which fish are retained, given and encounter with the net, is not equal across all size-classes of fish vulnerable to the gear. If not accounted for, size-selective sampling can introduce bias into corresponding estimates of growth and mortality. These are key parameters for many types of fisheries assessments (Ricker 1969). There has been an increasing need for robust estimates of growth and mortality for certain sport fish populations in Colorado given inquiries related to wild broodstock health, harvest regulations, nonnative piscivore suppression, and maintaining predator-prey balance.

Here, I developed a model to adjust the size-dependent catch of kokanee in vertical gill nets for differential retention probability. Vertical gill-netting of kokanee has increased recently due to the proliferation of gill lice in Blue Mesa Reservoir and data were readily available for developing these techniques. I assessed for potential generality across regions and gear types by comparing results of this work to those of Klein et al. (2019) who characterized the retention of kokanee in pelagic curtain nets in Idaho. Although applied to kokanee, the same methodology developed here will be used for multiple other ongoing research projects, particularly those related to Walleye.

METHODS:

Kokanee were sampled periodically during ice-free months in offshore waters of Blue Mesa Reservoir between 1995 and 2018 with a standard series of three 3 m wide × 55 m deep monofilament vertical gill nets. Each net was constructed with two side-by-side 1.5 m wide mesh panels extending the full range of depths. Thus, mesh sizes were paired on each net: 25-mm (0.28 mm diameter monofilament) and 38-mm (0.28 mm); 51-mm (0.28 mm) and 64-mm (0.28 mm); 76-mm (0.33 mm) and 102-mm (0.33 mm) stretch measure. Effort was equal across mesh sizes since all three nets were always fished overnight in each region of the reservoir.

The retention [$r_j(l)$] of kokanee in each 20 mm size-class l captured in each stretch mesh size j (m_j; Table 1) was estimated using the omnr.gillnet package in R (Walker et al. 2013). A total retention

curve [$r(l)$] for the combined gear (full suite of mesh sizes fished simultaneously) is given by: $r(l) = \sum_j r_j(l)/\max_l[\sum_j r_j(l)]$. The size-dependent catch-frequency adjusted for retention (N_l) from the combined gear is computed by dividing the observed catch total within each size-class (n_l) by the corresponding total retention value [$r(l)$] for that size-class.

Table 1. Numbers of kokanee captured by 20-mm size-class in six mesh sizes of vertical gill nets set periodically between 1995-2018 offshore in Blue Mesa Reservoir, Colorado.

Size-class (TL; mm)	Middle of bin (mm)	Mesh size (stretch; mm)						Total catch
		25	38	51	64	76	102	
100-120	110	5	1	0	0	1	0	7
121-140	130	6	0	0	0	0	0	6
141-160	150	1	1	0	0	0	0	2
161-180	170	0	16	0	0	0	0	16
181-200	190	3	17	0	1	0	0	21
201-220	210	0	6	11	1	0	0	18
221-240	230	0	1	51	3	0	2	57
241-260	250	0	1	64	21	2	0	88
261-280	270	0	0	15	42	2	0	59
281-300	290	0	2	7	53	12	1	75
301-320	310	0	0	5	54	36	2	97
321-340	330	0	0	2	41	63	3	109
341-360	350	0	0	2	12	29	3	46
361-380	370	0	3	5	12	31	4	55
381-400	390	1	4	4	15	37	23	84
401-420	410	0	1	3	11	28	21	64
421-440	430	1	2	2	7	6	23	41
441-460	450	0	0	1	2	4	6	13
461-480	470	0	0	0	0	0	4	4
481-500	490	0	0	0	0	1	0	1
Total catch		17	55	172	275	252	92	863

The omnr.gillnet package implements the approach of Millar and Fryer (1999) and fits five forms of gill-net retention curve (Table 2) to observed catches through maximum likelihood using generalized linear models (glm) with Poisson error and log link function. All models except for normal location, which assumed equal spread among mesh-specific retention curves, followed the principle of geometric similarity (Baranov 1914; Millar 1995; Table 2). This principle states that retention depends only on the relative geometry of the mesh and fish, and therefore, the mode and spread of retention curves should vary systematically in proportion to mesh size (Millar and Fryer 1999; Table 2).

The base models described above only account for the process of wedging (dependent on fish girth and mesh size), but tangling maintains an elevated probability of retention for large fish whose girth exceeds that of the mesh for all mesh sizes (Bromaghin 2005; Walker et al. 2013). To model both processes of capture, omnr.gillnet incorporates a tangle parameter (ω) that takes a value

between zero and one. As fish increase in length beyond the optimal size for a particular mesh (peak of curve), their probability of retention approaches ω rather than zero (Bromaghin 2005). Each of the five base models was fit with and without a tangle parameter, generating an *a priori* set of ten candidate models for comparison.

Table 2. Model equations and parameters (constants) for the five types of gill-net retention curve as described by Millar and Fryer (1999) fit to the kokanee catch data using the omnr.gillnet package in R. Note that omnr.gillnet outputs the square of the fitted value for some parameters and models (i.e., σ and k_2 for the normal and lognormal models; k_1, but not k_2, for the inverse Gaussian model).

Model (parameters)	Retention curve equation [$r_j(l) = \ldots$]
Normal location (k, σ^2)	$\exp\left(-\dfrac{(l - k \cdot m_j)^2}{2\sigma^2}\right)$
Normal scale (k_1, k_2^2)	$\exp\left(-\dfrac{(l - k_1 \cdot m_j)^2}{2k_2^2 \cdot m_j^2}\right)$
Lognormal (μ, σ^2)	$\dfrac{m_j}{l \cdot m_1}\exp\left(\mu - \dfrac{\sigma^2}{2} - \dfrac{\left(\log(l) - \mu - \log\left(\frac{m_j}{m_1}\right)\right)^2}{2\sigma^2}\right)$
Gamma (α, k)	$\left(\dfrac{l}{(\alpha - 1) \cdot k \cdot m_j}\right)^{\alpha - 1} \exp\left(\alpha - 1 - \dfrac{l}{k \cdot m_j}\right)$
Inverse Gaussian (k_1^2, k_2)	$\left(\dfrac{k}{l}\right)^{\frac{3}{2}} \exp\left\{\dfrac{-k_2}{2k_1^2 \cdot m_j}\left[\dfrac{(l - k_1 \cdot m_j)^2}{l} - \dfrac{(k - k_1 \cdot m_j)^2}{k}\right]\right\}$ where $k = \dfrac{k_1^2}{k_2} \cdot m_j\left(\sqrt{\dfrac{9}{4} + \dfrac{k_2^2}{k_1^2}} - \dfrac{3}{2}\right)$

The Poisson assumption (i.e., variance in catch numbers is equal to the mean) rarely holds in gill-net retention studies. More variation in catch numbers than is predicted by the model is usually found, which hinders statistical comparisons among models if not accounted for (Millar and Fryer 1999). Thus, models of best fit were identified from corrected quasi-Akaike information criterion scores (QAIC$_c$) referenced to the model with lowest QAIC$_c$ (denoted here as ΔQAIC$_c$) and computed from the quasi-deviance residuals [unsigned deviance adjusted for overdispersion ($\hat{c}$)] associated with each model fit (Walker et al. 2013). To assess information content and provide context for interpreting ΔQAIC$_c$ scores, a flat (null) model was also fit to the data. Flat models with ΔQAIC$_c$<10 are considered statistically indistinguishable from other models and indicate that the catch data contain little information on gill-net retention. Conversely, flat models with ΔQAIC$_c$ >10 indicate sufficient information for understanding the process of wedging. Similarly, if all no-

tangle models in addition to the flat model have $\Delta QAIC_c >10$, the data contain sufficient information to understand the combined processes of wedging and tangling. If the normal location model with or without a tangle parameter performs relatively well ($\Delta QAIC_c <10$), that would provide evidence against the assumption of geometric similarity.

RESULTS & DISCUSSION:

The catch of kokanee contained sufficient information to model the combined processes of wedging ($\Delta QAIC_c$ of flat model = 259.39) and tangling ($\Delta QAIC_c \geq 43.62$ for all no-tangle models; Table 3). In addition, the normal location model received little support ($\Delta QAIC_c = 51.85$ without tangle and 26.94 with tangle), consistent with the assumption of geometric similarity.

The normal scale model with a tangle parameter was best supported by the data ($\Delta QAIC_c = 0.00$), but the gamma model with a tangle parameter was functionally equivalent ($\Delta QAIC_c = 5.55$). Aside from the flat model, the no-tangle normal scale model was least supported ($\Delta QAIC_c = 105.23$), highlighting the importance of tangling in influencing the catch of pelagic-oriented kokanee in offshore vertical gill nets (Table 3).

Table 3. Fitted model parameters and associated model comparison and selection statistics for the five types of gill-net retention curve with and without a tangle parameter (ω) fitted to the kokanee catch data using the omnr.gillnet package in R. The QDev. represents the model deviance adjusted for overdispersion. The overdispersion parameter ($\hat{c}$) was 4.74. The $\Delta QAIC_c$ for the flat model was 259.39 and its weight was 4.42×10^{-57}. The best supported model has the lowest $QAIC_c$ and a $\Delta QAIC_c$ of zero (bold italics).

Model	Constants			QDev.	$QAIC_c$	$\Delta QAIC_c$	Model weight
	Parameter 1	Parameter 2	Parameter 3				
			No-tangle				
Normal location	$k = 4.63$	$\sigma^2 = 3{,}708.88$		105.36	160.98	51.85	5.15×10^{-12}
Normal scale	$k_1 = 5.040$	$k_2^2 = 1.78$		157.82	214.37	105.23	1.32×10^{-23}
Lognormal	$\mu = 4.82$	$\sigma^2 = 0.043$		96.76	152.76	43.62	3.15×10^{-10}
Gamma	$\alpha = 21.18$	$k = 0.24$		112.70	168.83	59.70	1.02×10^{-13}
Inverse Gaussian	$k_1^2 = 25.79$	$k_2 = 111.12$		100.02	156.15	47.02	5.77×10^{-11}
			Tangle				
Normal location	$k = 4.55$	$\sigma^2 = 1{,}991.00$	$\omega = 0.0391$	76.88	136.07	26.94	1.32×10^{-06}
Normal scale	$k_1 = 4.72$	$k_2^2 = 0.38$	$\omega = 0.0403$	*50.50*	*109.13*	*0.00*	*9.34×10^{-01}*
Lognormal	$\mu = 4.77$	$\sigma^2 = 0.023$	$\omega = 0.0320$	59.78	119.42	10.28	5.46×10^{-03}
Gamma	$\alpha = 46.077$	$k = 0.10$	$\omega = 0.0319$	55.49	114.68	5.55	5.84×10^{-02}
Inverse Gaussian	$k_1^2 = 23.11$	$k_2 = 200.91$	$\omega = 0.0323$	61.82	121.46	12.33	1.97×10^{-03}

Rather than incorporating a tangle parameter, Klein et al. (2019) fit bimodal curves to model the joint processes of wedging and tangling. The bimodal model was best supported by the data. The corresponding secondary mode of each $r_j(l)$ showed that the probability of tangling was low, but present across mesh sizes for large kokanee (those that exceeded the TL at peak retention for a given mesh) captured in pelagic curtain nets in Idaho. This agreed with kokanee captured in vertical gill nets in Colorado (Figure 1). The estimated value for the best fit tangle parameter (ω) was 0.0403. Similarly, visual inspection indicated strong congruence between the wedging portions of each $r_j(l)$, particularly the TL at peak retention (Figure 1). This included the $r_j(l)$ for 13-mm and 19-mm mesh. These mesh sizes were not modeled explicitly in this study, but were reliably predicted from the principle of geometric similarity. The spread associated with each $r_j(l)$

for Colorado slightly exceeded that of Idaho for the larger mesh sizes, but this consistent pattern did not translate into notable differences when integrating over each $r_j(l)$ to develop the $r(l)$ curves. There was high correlation ($r = 0.98$; $P \ll 0.001$) between the $r(l)$ values of Idaho and those of Colorado over the 50-430 mm TL range and the values followed a 1:1 relationship.
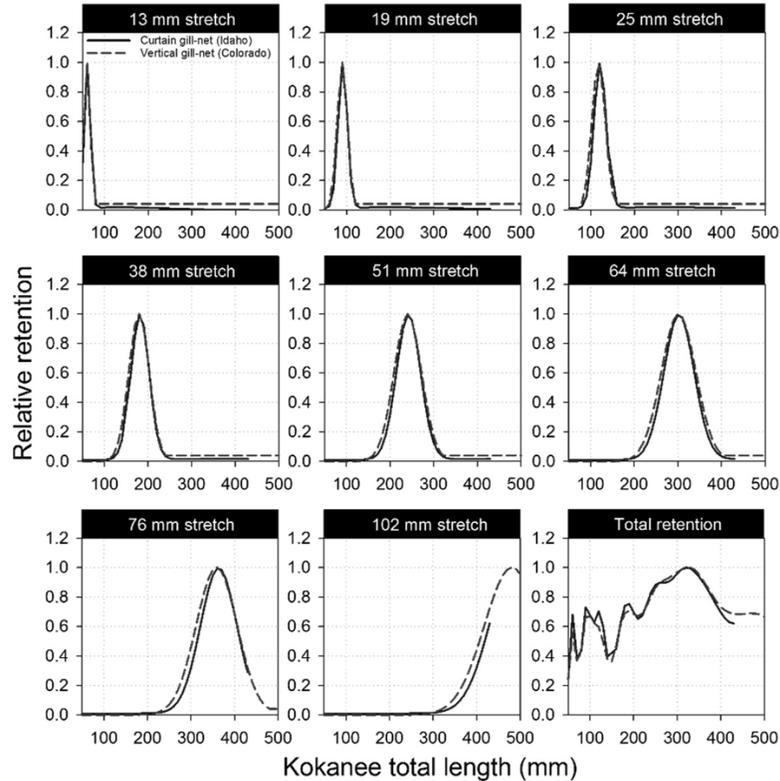

Figure 1. Mesh-specific [$r_j(l)$] and total [$r(l)$] retention curves for pelagic-oriented kokanee 50-500 mm TL based on the best supported normal scale model with a tangle parameter from the present study (dashed lines), and the bimodal model of Klein et al. (2019) (solid lines). Corresponding mesh sizes (stretch measure in mm) are noted on each panel. The $r_j(l)$ for Colorado kokanee in the 13-mm and 19-mm mesh sizes were not modeled explicitly in this study, but predicted based the principle of geometric similarity for comparison to Klein et al. (2019).The $r(l)$ from Klein et al. (2019) shown was not adjusted for size-dependent probability of encounter.

The size-structure of a fish population reflects the interactive processes of recruitment (natural or hatchery), growth, and mortality (harvest, predation or other). Because of this, size-structure is fundamental to quantifying and managing (e.g., through harvest regulations, predator suppression, or adjusting stocking practices) the often complex interactions among kokanee, their predators (native or introduced), and anglers. For example, quantifying kokanee population dynamics and productivity (Hansen et al. 2010; Pate et al. 2014; Corsi et al. 2019), the susceptibility of kokanee to different introduced predators (Schoen et al. 2012; Hansen et al. 2019), emerging parasite-host dynamics involving *Salmincola* (Hargis et al. 2014), recreational harvest dynamics (Askey and Johnston 2013), and predicting spawner escapement for informing wild-spawn and hatchery operations (Baldwin and McLellan 2008) requires minimally biased information on size- and age-structure. Although retention models alone likely do not account for all processes influencing the size-selectivity of experimental gill nets, they remove some bias and strengthen evaluations like those listed above.

There was strong congruence between the total retention values (integrated over all mesh sizes) estimated by the Idaho model and by the Colorado model, despite using different types of gill nets to catch kokanee. This result indicates that the retention of fish in specific mesh sizes may be largely conserved across regions and gear configurations. So, retention models may not need to be reservoir- or gear-specific to be useful. These properties enable practitioners to easily adjust length-frequency distributions for bias arising from size-dependent retention when minimally biased estimates of size-structure are needed for addressing management or research questions.

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RESEARCH PRIORITY: Evaluating the effectiveness of angler harvest incentive tournaments for suppressing nonnative piscivores in sensitive locations.

OBJECTIVES:

Assess the response of Smallmouth Bass and anglers to incentivized fishing tournaments conducted to date on Ridgway and Elkhead Reservoirs.

INTRODUCTION:

There are no documented attempts to suppress invasive Smallmouth Bass using a cost effective angler incentive program. Yet, this approach allows anglers to support management and could be effective in small systems alone or in conjunction with other methods. Colorado Parks and Wildlife (CPW) has conducted incentivized angler harvest tournaments to suppress Smallmouth Bass in Ridgway (SW Colorado) and Elkhead (NW Colorado) Reservoirs over the last 6 years to reduce potential entrainment and support conservation of native fish in critical habitat downstream. At the onset of these programs, age-structured simulation models informed by field data demonstrated that anglers could reduce the abundance of adult Smallmouth Bass by upwards of 95% over a ten-year period, assuming (1) nearly equal fishing effort during the tournaments each year, (2) catchability increases as abundance declines, and (3) no compensatory responses (e.g., faster growth and earlier maturation) that enhance recruitment are realized (Hansen 2018). Here, I report on the observed rather than simulated responses of Smallmouth Bass and of anglers over the 2015-2020 period in Ridgway and 2017-2020 period in Elkhead. I use the longer time-series of observed data from Ridgway Reservoir to assess key assumptions of the simulation models.

METHODS:

Tournament structure, monitoring approach, simulation model development and pertinent literature are detailed in Hansen (2018). In brief, extensive sampling is conducted annually to monitor the response of Smallmouth Bass and anglers to the incentivized fishing tournaments. Mark-recapture methods are used to estimate the abundance of adult ($\geq$150 mm total length; TL) and juvenile (<150 mm TL) Smallmouth Bass wherein fish are marked prior to the tournament using boat electrofishing, then recaptured throughout the tournament by anglers. During the tournaments, lengths of all fish captured are measured, and most of these fish (generally >95%) are donated to CPW for purposes of research. Otoliths for determining growth, age-structure and maturity status are collected from a systematic random subsample of donated fish. Potential shifts and variation in Smallmouth Bass recruitment are assessed using standardized fall boat electrofishing surveys (if possible) when new age 0 fish become fully vulnerable to capture. Total fish harvested and total 'effective' fishing effort in hours (defined as time spent fishing wherein at least one fish is harvested) are tallied for each angler individually.

RESULTS & **DISCUSSION**:

Age-structured simulations models were developed to predict the response of Smallmouth Bass to

angler harvest, develop reference points for harvest rate (i.e., threshold for unsustainability) and to assess the potential biological effectiveness of the tournaments when conducted during different times of year and over different durations to help optimize their design within the constraints of other management obligations. First, these models highlighted the importance of angler catchability, and whether it varies as a function of Smallmouth Bass abundance. Under some circumstances, catchability may increase as fish abundance declines (Peterman and Steer 1981; Shuter et al. 1987), which improves the potential outlook of suppression efforts (Figure 1).
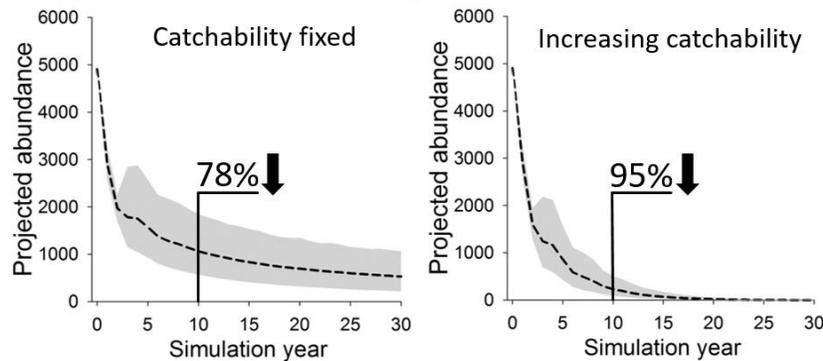

Figure 1. Simulated mean abundance (dashed lines) of adult Smallmouth Bass in Ridgway Reservoir assuming angler catchability is fixed through time (left panel) versus assuming angler catchability increases as the abundance of Smallmouth Bass declines (right panel). Shaded regions represent 95% confidence intervals. Values represent the percent decline in starting abundance after 10 years of suppression by anglers. Simulations were based on fishing effort and catch levels observed during the 2017 tournament (24 days in July rather than 10 days in June).

Second, simulation models indicated that annual harvest rates of ≥40% and ≥35% were 'unsustainable' over the long-term (i.e., sufficient to drive the population toward 'zero') for Smallmouth Bass in Ridgway and Elkhead, respectively. These reference points enable rapid assessment of what was achieved during the tournament each year versus what is required for continued suppression. To date, the adult harvest rate obtained during three of the six tournaments conducted at Ridgway have been unsustainable, whereas harvest rates from all tournaments at Elkhead have remained within the 'sustainable' realm, but sufficient to reduce the population to a lower abundance level (Figure 2).
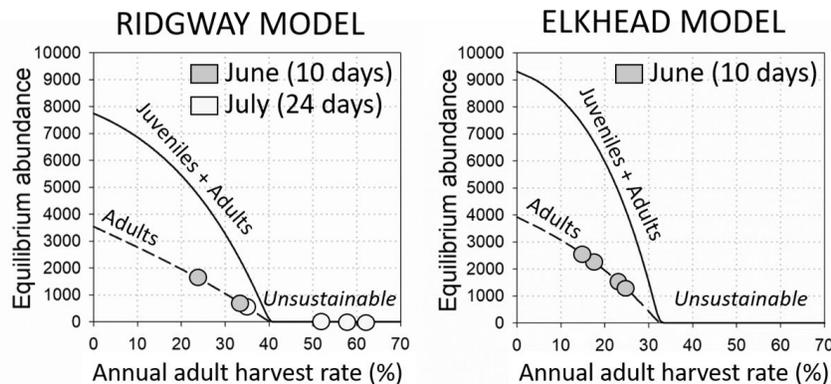

Figure 2. Predicted long-term equilibrium abundance of Smallmouth Bass as a function of the annual adult harvest rate based on the age-structured simulation model developed for Ridgway Reservoir (left panel) and the model for Elkhead Reservoir (right panel). Points denote the adult harvest rates achieved during all tournaments to date.

Trends in the time-series of pre- and post-tournament abundance estimates for Smallmouth Bass in each reservoir align with what would be expected based on the observed harvest rates and the corresponding model predictions above. The difference between the starting abundance and the 2020 post-tournament abundance of adult Smallmouth Bass reflects an 80% decline in Ridgway and a 61% decline in Elkhead (Figure 3).
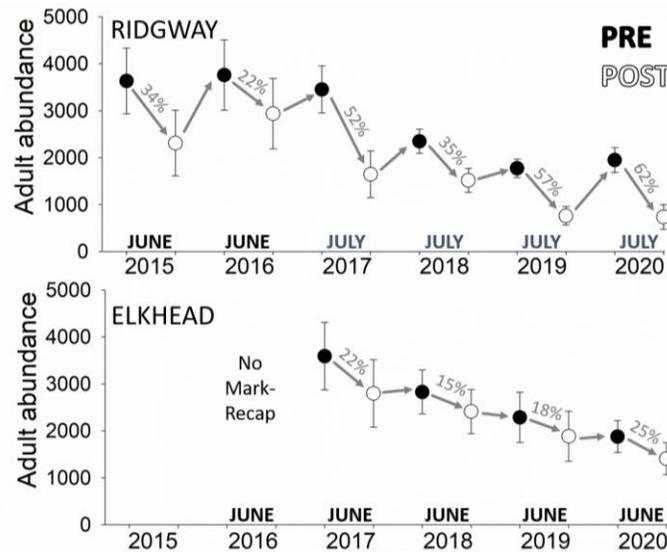

Figure 3. Time-series of pre- and post-tournament abundance estimates for adult Smallmouth Bass in Ridgway Reservoir (top panel) and Elkhead Reservoir (lower panel). Percent values denote the adult harvest rate achieved during each fishing tournament. Error bars represent 95% confidence intervals.

Interestingly, significant bounce-back of adult fish occurred between 2019 and 2020 in Ridgway (Figure 3), which had not been observed to the same extent the previous two years. However, anglers were able to somewhat compensate for this bounce-back by achieving an adult harvest rate of 62% during the 2020 tournament—the highest rate observed to date. This bounce-back corresponded with a relatively strong year-class of age 0 fish observed during the 2017 standard fall boat electrofishing survey (Figure 4).
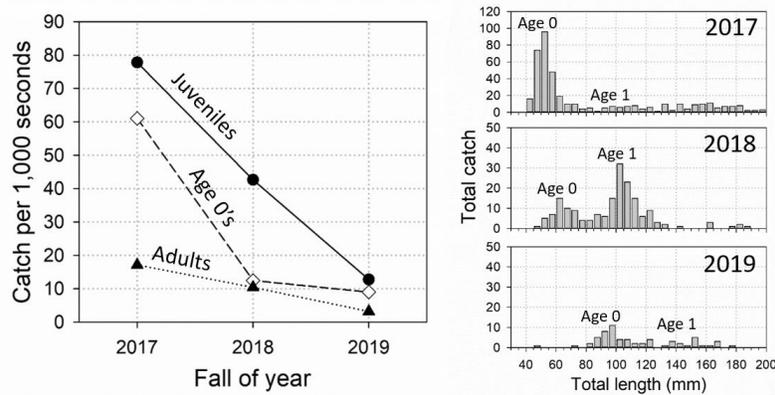
Figure 4. Catch rates of juvenile (<150 mm TL), adult (≥150 mm TL) and age 0 Smallmouth Bass during standardized fall boat electrofishing surveys over the 2017-2019 period in Ridgway Reservoir (left panel). The right panels portray length-frequency distributions of juvenile fish captured during each survey year and used to parse out age 0 fish. Age designations on the length-frequency histograms were confirmed from a subset of sectioned otoliths.

Based on the observed growth rates of Smallmouth Bass, the 2017 year-class would have fully recruited into the adult size-range (≥150 mm TL) in 2020. Relative to 2017, the strength of the 2018 and 2019 year-classes were much reduced, which could lead to less bounce-back in coming years. However, the growth rate of young fish has increased recently (Figure 5), and they are now larger in fall than previously observed (Figure 4). Whether this reflects some inherent density-dependent process or was driven by environmental conditions in the reservoir or both is uncertain. Regardless, larger body size in fall could improve the overwinter survival of age 0 fish and perhaps compensate to some extent for their reduced numbers.
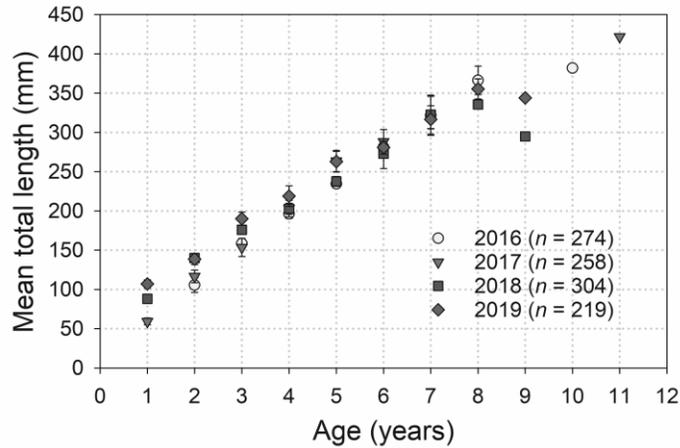

Figure 5. Mean length-at-age estimated from sectioned otoliths removed from systematic random subsamples of Smallmouth Bass captured and donated to research during fishing tournaments over the 2016-2019 period in Ridgway Reservoir. Errors represent ± 1SE. Estimates are for male and female fish combined as there were no sex-specific differences in growth.

Despite some observed shifts in the growth rate of young fish in recent years at Ridgway, age-at-maturity has not changed, particularly for female fish (Figure 6). Logistic regression models fit to the age-at-maturity data with and without year as a factor were functionally equivalent for both males and females based on Akaike's Information Criterion. Similar growth and maturity analyses for Smallmouth Bass in Elkhead Reservoir and sample processing for fish captured in 2020 have not been completed yet.
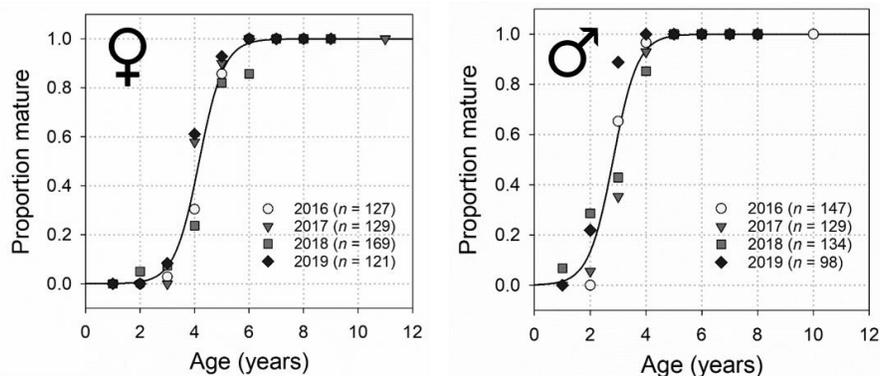

Figure 6. Proportion mature-at-age estimated for female (left panel) and male (right panel) Smallmouth Bass captured by anglers during fishing tournaments over the 2016-2019 period in Ridgway Reservoir. Lines represent logistic regression models fitted through data pooled across years.

Angler participation and total effective fishing effort have differed between reservoirs. First, the number of registered anglers has declined at Ridgway since the onset of tournaments. The reverse pattern was observed at Elkhead, although participation was reduced in 2020 compared to previous years. Similarly, fishing effort has declined at Ridgway, but stable at Elkhead. Despite reductions in fishing effort at Ridgway, the adult harvest rates achieved have remained elevated (Figure 7).
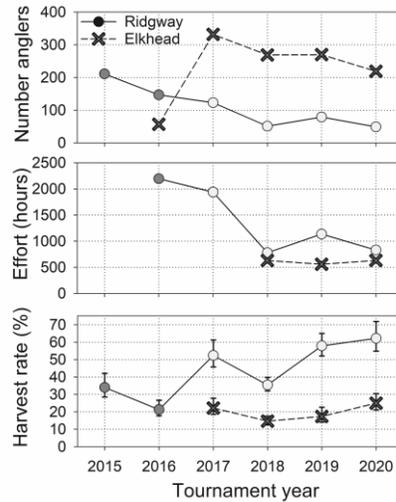

Figure 7. Time-series of angler participation (top panel), effective fishing effort (middle panel) and harvest rate (bottom panel) observed during each fishing tournament to date at Ridgway (circles) and Elkhead (x's) Reservoirs. Open circles for Ridgway reflect 24-day tournaments conducted in July, whereas closed circles represent 10-day tournaments conducted in June. All tournaments at Elkhead have been for 10 days in June. Error bars for harvest rate represent 95% confidence intervals.

Harvest rates have remained elevated despite reduced participation and fishing effort for two reasons. First, the catchability of Smallmouth Bass has increased through time at Ridgway and Elkhead (Figure 8). One explanation is that Smallmouth Bass concentrate within key habitats and are not distributed randomly throughout the reservoir, which aligns with patterns in the catch from boat electrofishing surveys. Thus, when aggregations are found, anglers can maintain high catch rates even though the overall abundance of fish has declined. These results align with the assumption of 'increasing catchability' from the preliminary model simulations above (Figure 1).
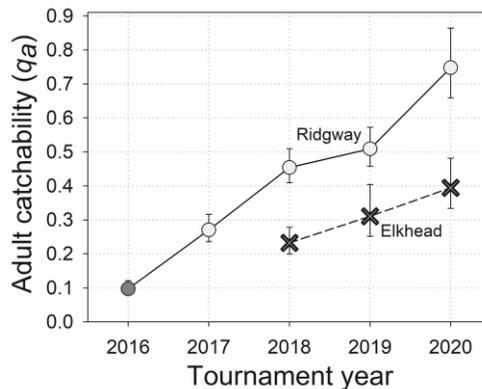

Figure 8. Estimated angler catchability of adult Smallmouth Bass through time in Ridgway and Elkhead Reservoirs. Values represent the proportion of adult fish harvested after a standardized 1,000 hours of effective fishing effort.

Second, only a small subset of anglers harvest the majority fish, devote the most fishing effort, and are generally the most effective. For example, the top ten anglers harvested 84% and 73% of all Smallmouth Bass during the 2019 tournament at Ridgway and Elkhead, respectively (Figure 9). This pattern has been consistent across years. Thus, the mere presence of these 'most valuable players' or MVPs buffer harvest to reductions in overall participation and fishing effort. There is indication that these MVPs are largely returning locals, so they may be learning and contributing to higher catchability through time as well (Figure 8). Providing additional incentives to the MVPs may be one approach for elevating fishing effort and harvest rates even further.
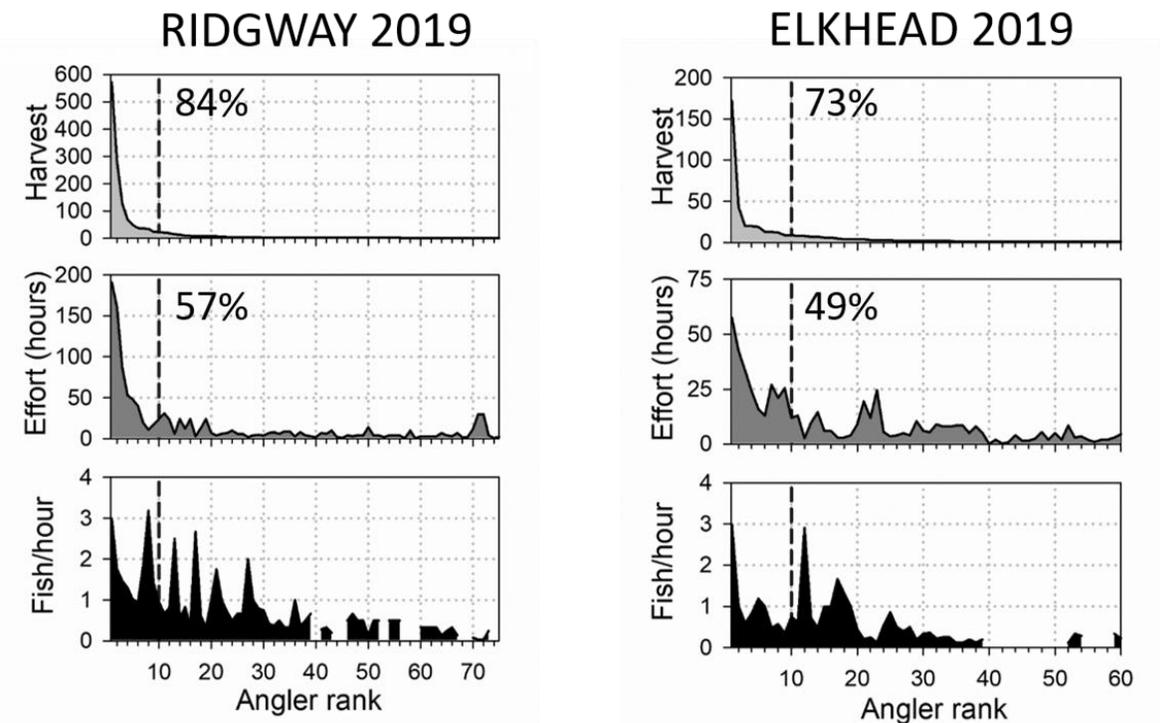
Figure 9. Total harvest, effective fishing effort and catch rates achieved by each registered angler during the 2019 fishing tournaments on Ridgway (left panels) and Elkhead (right panels) Reservoirs. Anglers are ranked from highest to lowest based on total fish harvested. Vertical lines and values denote the percentage of total harvest and fishing effort contributed by the top ten anglers. Only showing the top 60 anglers from Elkhead.

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RESEARCH PRIORITY: Calibration of Fall Walleye Index Netting (FWIN) and broodstock assessments.

OBJECTIVES:

Assess utility of Fall Walleye Index Netting as a standardized sampling protocol for estimating the density and size-structure of and monitoring recruitment in key Walleye reservoirs (broodstocks and other important fisheries). Use this method to estimate and compare demographics among populations, discern potential limiting factors, and evaluate appropriateness of harvest regulations where requested.

INTRODUCTION:

Walleye are highly sought after sport and food fish in the state of Colorado. Unlike in the upper Colorado River Basin on the western slope—which contains critical habitat for four endemic species of native fish—Walleye can be managed for directly as a predatory sport fish in reservoirs east of the continental divide. Given generally poor natural-recruitment and high fishing pressure, most Walleye fisheries are sustained through annual stocking of fry in early April and pond-reared 1-2 inch fingerlings later in May or early June. Statewide stocking requests are supported through spring egg-take operations from wild broodstocks in three reservoirs: Chatfield, Cherry Creek and Pueblo. Current harvest regulations (18 inch minimum length limit; daily bag limit = 3-5 depending on reservoir; only one >21 inches is allowed) on each of the broodstock reservoirs are restrictive to protect larger females essential for meeting egg collection goals and statewide stocking schedules. However, anglers have expressed interest in relaxing regulations at Pueblo Reservoir to allow harvest of smaller fish given a perceived lack of 'keepers' over the 18 inch minimum length limit. In addition, spring egg-takes at Chatfield Reservoir have been relatively poor in recent years, placing greater burden on Pueblo and Cherry Creek Reservoirs.

Given recent questions from anglers regarding harvest regulations at Pueblo and concerns over poor egg-takes at Chatfield, we initiated a new study to characterize the population demographics of each Walleye broodstock to (1) help inform population models for objectively assessing the appropriateness of different harvest regulations, and (2) make standardized comparisons among populations to help discern potential factors limiting Walleye in Chatfield vs. elsewhere and to identify potential management solutions or areas in need of additional research. Central to these objectives was estimating the density and size- and age-structure of each Walleye population in a way that enabled reliable comparisons among them. However, existing survey data was either limited or conducted during different seasons and did not allow for appropriate cross-reservoir evaluations or for the estimation of Walleye density.

Therefore, we explored a new standardized sampling technique—Fall Walleye Index Netting (FWIN; Giacomini et al. 2020)—as a means to control for sampling season and interannual differences in reservoir surface elevation, better integrate catch over time and space to develop minimally-biased estimates of size- and age-structure, and to rapidly estimate the density of adult Walleye in each reservoir. In addition to assessing the brood waters, developing a standardized sampling protocol for Walleye should benefit triploid Walleye research on the western slope of

Colorado by providing a means for quickly estimating the proportion of triploids vs. diploids in existing mixed populations or for monitoring newly stocked triploid populations (see final section of report). Lastly, we conducted a FWIN survey on Horsetooth Reservoir—supported through natural reproduction only—for comparison to the brood waters and to inform ongoing research regarding food web interactions with Rainbow Smelt (will be reported on next year; see Hansen 2018 and Treble and Hansen 2019). The FWIN protocol is not meant to replace existing spring or fall gill-netting surveys and the time-series those have generated. Rather, it is meant to compliment those surveys and provide a robust tool for periodic use when more in-depth assessment is required to address emerging questions.

METHODS:

Like Summer Profundal Index Netting for assessing Lake Trout populations (Sandstrom and Lester 2009), FWIN is a standardized gill-netting protocol for rapidly estimating the density and size-structure of Walleye populations at a time of year that also enables assessment of year-class strength as age 0 fish of either stocked- or natural-origin generally recruit to the sampling gear by that time (Giacomini et al. 2020; A. G. Hansen, unpublished data). A minimum number of standard FWIN nets (based on lake or reservoir size) are fished for 24 hours in two depth-strata (2-5 m and 5-15 m) weighted by the relative proportion area of each. Set locations are randomized prior to implementation of the survey. Sampling is conducted in the fall when water surface temperatures range from 10-15°C. The gillnets are 1.8 m deep × 60.8 m long and are composed of eight 7.6 m long mesh panels ranging from 13-76 mm bar measure and arranged in sequential order (13-, 19-, 25-, 32-, 38-, 51-, 64- and 76-mm; Morgan 2002).

Giacomini et al. (2020) estimated the catchability ($\hat{q}$) of Walleye ≥350 mm total length (TL) and corresponding variance by relating catch-per-unit-effort—mean, area-weighted number of fish caught per gill-net set or 'gang' following the FWIN protocol—to independent estimates of Walleye density from mark-recapture surveys in twelve Ontario/Quebec lakes. The lakes ranged in mean and max depths, but generally aligned with the morphometry of numerous reservoirs on Colorado's Front Range. Random variation among lakes was important, but Giacomini et al. (2020) provided a global estimate of catchability ($\hat{q}$ = 1.044 ha/gang; variance = 0.2268; 95% CI = 0.753-1.448) that can be used to estimate fish density (fish ≥350 mm TL/ha) and corresponding uncertainty in a new lake or reservoir. In addition, they provided methods for extending to different size-ranges by scaling the density estimated by $\hat{q}$ based on size-dependent retention probabilities (see Hansen 2019) specific to the FWIN nets. Thus, FWIN could be a powerful tool, but first required ground-truthing to evaluate whether the catchability of Walleye in Colorado Reservoirs was similar to those in the Canadian lakes or whether additional corrections were needed.

We conducted FWIN on Pueblo (10/29/2018-11/1/2018; N = 15 total sets; 1,551.97 ha at time of survey), Cherry Creek (10/23/2019-10/25/2019; N = 11 total sets; 315.66 ha), Chatfield (10/28/2019-10/30/2019; N = 14; 571.42 ha) and Horsetooth (11/4/2019-11/6/2019; N = 14 total sets; 699.69 ha) Reservoirs. Surface water temperatures were within the 10-15°C range on each reservoir. For each survey, sagittal otoliths were collected from all or systematic random subsample of fish captured for age, growth and mortality assessment using standard methods (Isely and Grabowski 2007; Ogle 2016). Sex and maturity status were also noted (Duffy et al. 2000).

Prior to FWIN on Cherry Creek and Chatfield, spring mark-recapture surveys were completed to help assess the appropriateness of the global $\hat{q}$ estimated by Giacomini et al. (2020) for use in Colorado. During the 2019 wild spawn operations (mid-March through early April), post-spawn male and female Walleye were fin-clipped and released after a recovery period to ensure only healthy individuals were marked. Short-term mortality for female Walleye handled during artificial spawn operations is typically low (Blackwell et al. 2018), so we did not correct numbers marked for potential-post release mortality. In May 2019, after spawning was complete and fish were redistributed, we revisited each reservoir and used short-term (30 minutes to 1 hour) gill-net sets (both FWIN and multifilament-nylon spawn nets combined) at night to recapture previously marked individuals. Because catch during the recapture event at Chatfield was low, additional data were collected by a local fishing guide in June 2019.

RESULTS & **DISCUSSION**:

Mark-recapture estimates of abundance.—During the 2019 spring spawn operations on Cherry Creek and Chatfield Reservoirs, 1,578 and 259 adult Walleye ≥400 mm TL were marked and released, respectively. On Cherry Creek, 212 total and 26 marked adult Walleye were encountered during the recapture event. The Chapman estimator (Hayes et al. 2007) yielded a population estimate ± 95% CI of 12,456 ± 4,275 adults (39.5 ± 13.5 adults/ha). On Chatfield, 64 total and 7 marked adult Walleye were encountered, yielding an estimate of 2,112 ± 1,272 adults (3.7 ± 2.2 adults/ha). For reference, the estimated density of adult Walleye in Cherry Creek fell well above the 75th percentile of densities (23.9 adults/ha) observed from Walleye populations across North America (Baccante and Colby 1996). Conversely, the estimated density of adult Walleye in Chatfield fell well below the 25th percentile (8.1 adults/ha).

The length-frequency distributions of Walleye marked during the spring spawning operations closely resembled those of fish encountered during the recapture event on both reservoirs. Thus, no additional corrections were needed to remove potential size-related bias in the estimation of abundance (Ricker 1975). Given the large disparity in estimated densities, which spanned nearly the full spectrum observed from Walleye populations elsewhere (Baccante and Colby 1996), a reliable appraisal of $\hat{q}$ following the FWIN protocol derived by Giacomini et al. (2020) was possible. However, because $\hat{q}$ was only estimated for fish ≥350 mm TL, we needed to incorporate size-dependent gill-net retention probabilities to appropriately scale $\hat{q}$-based densities for estimating the abundance of fish ≥400 mm TL estimated from mark-recapture. Although size-dependent retention probabilities for FWIN nets have been published by Walker et al. (2013) for Walleye in Ontario, we estimated these again following the methods of Hansen (2019) by combining catch data across all four reservoirs examined here (Pueblo, Cherry Creek, Chatfield and Horsetooth; N = 1,990 fish ranging from 110-731 mm TL) to ensure congruence between regions. Total retention curves derived from both regions were nearly identical (Figure 1), supporting the broad applicability of these values.

FWIN estimates of density.—On Pueblo Reservoir, 15 individual FWIN net sets (four within 2-5 m and remainder within 5-15 m) captured 627 Walleye ranging in size from 145-664 mm TL (mean ± SD = 356 ± 82 mm). The FWIN protocol called for a minimum of 18 sets on Pueblo. However, given the high and consistent catch rates, we decided to fish three nets in random

locations at depths >15 m to assess whether we were missing a fraction of the population. Only three Walleye were captured in deeper depths. The mean, area-weighted estimate of CPUE for fish ≥350 mm TL was 27.91/gang. This yielded a density estimate of 26.73 fish/ha (lower 95% CI = 18.46; upper = 37.08) after applying the $\hat{q}$ derived by Giacomini et al. (2020). After accounting for the size-dependent retention of fish in the FWIN gear, the estimated density of fish ≥400 mm TL was 14.23 fish/ha (lower = 9.82; upper = 19.74). Based on the surface area of Pueblo Reservoir at the time of sampling, corresponding abundance estimates were 41,489 (lower = 28,642; upper = 57,553) and 22,086 fish (lower = 15,248; upper = 30,638), respectively.
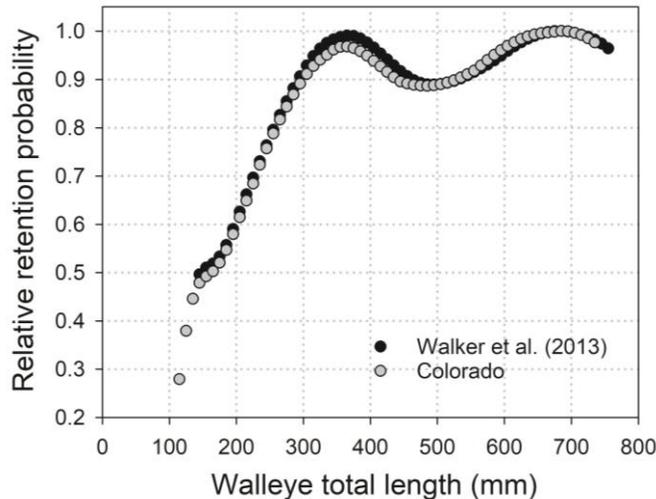

Figure 1. Total size-dependent gill-net retention curves estimated for every 10 mm length-bin by Walker et al. (2013) for Walleye captured in FWIN nets in Ontario (black dots) and from the present study by integrating catch data from Pueblo, Cherry Creek, Chatfield and Horsetooth Reservoirs in Colorado (gray dots).

On Cherry Creek Reservoir, 11 individual FWIN net sets (six within 2-5 m and five within 5-15 m) captured 1,016 Walleye ranging in size from 152-725 mm TL (mean ± SD = 320 ± 93 mm). The mean, area-weighted estimate of CPUE for fish ≥350 mm TL was 31.83/gang. This yielded a density estimate of 30.49 fish/ha (lower 95% CI = 21.05; upper = 42.29) after applying the $\hat{q}$ derived by Giacomini et al. (2020). After accounting for the size-dependent retention of fish in the FWIN gear, the estimated density of fish ≥400 mm TL was 18.79 fish/ha (lower = 12.97; upper = 26.07). Based on the surface area of Cherry Creek Reservoir at the time of sampling, corresponding abundance estimates were 9,623 (lower = 6,644; upper = 13,349) and 5,933 fish (lower = 4,096; upper = 8,230), respectively.

On Chatfield Reservoir, 14 individual FWIN net sets (seven within 2-5 m and seven within 5-15 m) captured 181 Walleye ranging in size from 110-714 mm TL (mean ± SD = 365 ± 76 mm). The mean, area-weighted estimate of CPUE for fish ≥350 mm TL was 9.48/gang. This yielded a density estimate of 9.08 fish/ha (lower 95% CI = 6.27; upper = 12.59) after applying the $\hat{q}$ derived by Giacomini et al. (2020). After accounting for the size-dependent retention of fish in the FWIN gear, the estimated density of fish ≥400 mm TL was 3.39 fish/ha (lower = 2.34; upper = 4.70). Based on the surface area of Chatfield Reservoir at the time of sampling, corresponding abundance estimates were 5,187 (lower = 3,581; upper = 7,195) and 1,935 fish (lower = 1,336; upper = 2,685), respectively.

On Horsetooth Reservoir, 14 individual FWIN net sets (five within 2-5 m and nine within 5-15 m) captured 161 Walleye ranging in size from 395-731 mm TL (mean ± SD = 515 ± 60 mm). The mean, area-weighted estimate of CPUE for fish ≥350 mm TL was 11.63/gang. This yielded a density estimate of 11.14 fish/ha (lower 95% CI = 7.69; upper = 15.45) after applying the $\hat{q}$ derived by Giacomini et al. (2020). After accounting for the size-dependent retention of fish in the FWIN gear, the estimated density of fish ≥400 mm TL was 11.08 fish/ha (lower = 7.65; upper = 15.36). In order to compare to mark-recapture estimates conducted during the mid-1990s (Johnson and Goettl 1999), we also computed the density of fish ≥450 mm TL: 10.37 fish/ha (lower = 7.16; upper = 14.39). These estimates were all similar because very few fish <400 mm TL were captured in the FWIN survey. Based on the surface area of Horsetooth Reservoir at the time of sampling, corresponding abundance estimates were 7,795 (lower = 5,381; upper = 10,813), 7,749 (lower = 5,350; upper = 10,750) and 7,257 fish (lower = 5,010; upper = 10,066), respectively.

Comparison and FWIN to mark-recapture.—Congruence between the FWIN and mark-recapture based estimates of adult Walleye abundance was dependent on population size-structure and density and whether the population was supported through annual stocking (Chatfield, Cherry Creek and Pueblo) or through natural reproduction (Horsetooth). High congruence was observed between estimates derived for Chatfield (fish ≥400 mm TL) and Horsetooth (fish ≥450 mm TL to align with Johnson and Goettl 1999). Despite being stocked annually, the estimated density of Walleye in Chatfield was the lowest out of the four reservoirs examined. Estimates for Horsetooth—driven by natural reproduction only—were approximately 3-fold higher than Chatfield (Figure 2).
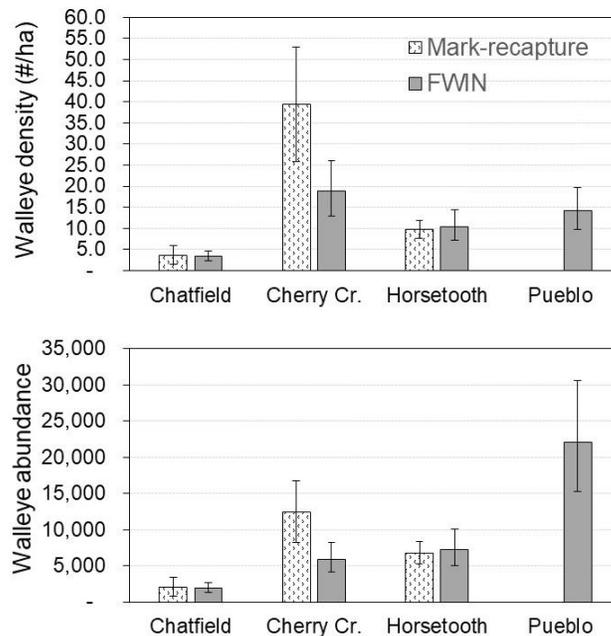
Figure 2. Comparisons between FWIN and mark-recapture based estimates of adult Walleye density (top panel) and abundance (bottom panel) in four Colorado Reservoirs. For Chatfield, Cherry Creek and Pueblo, estimates are for fish ≥400 mm TL. For Horsetooth, estimates are for fish ≥450 mm TL to align with historic mark-recapture studies conducted by the CDOW during the mid-1990s and reported by Johnson and Goettl (1999). The mark-recapture bar for Horsetooth is not a year-specific estimate. Rather, it represents the general range of values (5,300-8,300 fish) from estimates derived over the 1992-1995 period as reported by Johnson and Goettl (1999).

Poor congruence was observed between estimates (fish ≥400 mm TL) derived for Cherry Creek. The FWIN estimate was ~50% lower than the mark-recapture estimate, and was also similar to the FWIN estimate for Pueblo (Figure 2). Both populations are supported through annual stocking. Distinct patterns emerged after conducting FWIN on Cherry Creek and Pueblo that separated these reservoirs from Chatfield and Horsetooth which may explain poor congruence at Cherry Creek and have implications for the density estimates derived for Pueblo (no mark-recapture information available).

The catch of fish ≤350 mm TL—primarily age 0 and age 1 individuals—was high when compared to Chatfield. No fish ≤350 mm TL were captured in Horsetooth and the population was largely comprised of adults ≥age 5. Conversely, the catch of adult fish ≥450 mm TL was relatively low in all reservoirs except for Horsetooth, despite a lower density of adult fish in Horsetooth based on past and present mark-recapture surveys. The low catch of large adults in Chatfield was expected, but unexpected in Cherry Creek and Pueblo based on data from the spawn operations and the mark-recapture survey.
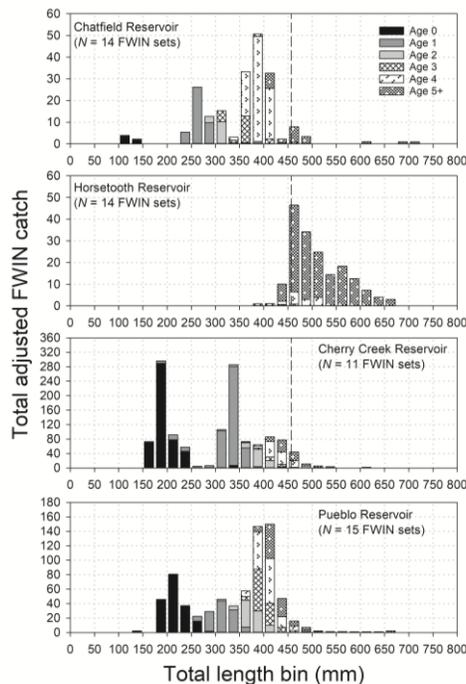

Figure 3. Length- and age-frequencies of Walleye captured during FWIN surveys on three Colorado reservoirs supported through annual stocking (Chatfield, Cherry Creek and Pueblo) and one supported through natural reproduction (Horsetooth). Catch-at-age for Walleye ≥age 5 were combined because that was when growth between male and female Walleye generally converged in all populations. Note the difference in y-axes. The number of FWIN net sets conducted on each reservoir are noted to indicate overall sampling effort. The dashed line reflects the 18 inch minimum length limit associated with the brood waters (no size-restrictions on Horsetooth; daily bag limit = 5 fish).

The Horsetooth survey demonstrated that large adult Walleye are vulnerable to capture in the FWIN gear, which was also reflected in the estimated size-dependent retention probabilities (Figure 1). In addition, Giacomini et al. (2020) noted a positive association between q and the mean length of Walleye surveyed. Thus, it seems retention of large adult fish in FWIN gear is reduced in highly dense populations supported through annual stocking, leading to conservative

estimates of abundance. The populations examined by Giacomini et al. (2020) were all supported through natural reproduction and the estimated densities of Walleye ≥350 mm TL from mark-recapture were all <30 fish/ha. The estimated density of adult Walleye ≥400 mm TL from mark-recapture in Cherry Creek approached 40 fish/ha. The nets were seemingly saturated with highly abundant, young individuals, so gear detection and avoidance from the less abundant older fish was possible. Because similar observations occurred at Pueblo, we can probably assume that the abundance estimate derived from FWIN for adult Walleye there is also conservative and should be considered in future assessments of alternative harvest regulations.

Based on the catch in and biological samples collected from FWIN nets, the growth and relative year-class strength of young fish (age 0 and age 1) in Chatfield was low compared to Cherry Creek and Pueblo Reservoirs. The estimated size of age 1 fish in spring for Chatfield was approximately half that estimated for Cherry Creek and Pueblo (Figure 4). Although the recent fry and fingerling (not done every year) stocking rates for Cherry Creek (mean density ± SD over 2010-2018: 12,518 ± 1,173 fry/ha and 44 ± 9 fingerlings/ha) and Pueblo (7,585 ± 824 fry/ha and 10 ± 7 fingerlings/ha) have been higher than those at Chatfield (5,362 ± 229 fry/ha and 28 ± 5 fingerlings/ha), the disparity in catch was greater than expected from differences in stocking rates alone—indicating a potenital early feeding, growth and survival bottleneck for stocked fish in Chatfield. In addition, the estimated mean size-at-age for older female and male Walleye and average expected life-time growth in Chatfield was similar to or exceeded conspecifics in the other brood waters, further supporting the presence of a potenital ecological bottleneck early in life. These patterns were reflected in the estimated parameters of the von Bertalanffy growth functions fit to the individual size-at-age data collected from each reservoir. The L_{inf} parameter (asymptote of curve) estimated for females and males in Chatfield exceeded those of the other populations. Conversely, the K parameters (govern curvature and how quickly asymptote is reached) were less than the other reservoirs (Figure 4). Because adequate early feeding and growth is vital to successful walleye recruitment (Madenjian and Carpenter 1991), examining the progression of spring-early summer food supply in relation to when fry vs. fingerlings are typically stocked is warranted. Mortality estimation for all reservoirs is still in progress and could uncover other potenital limitations.
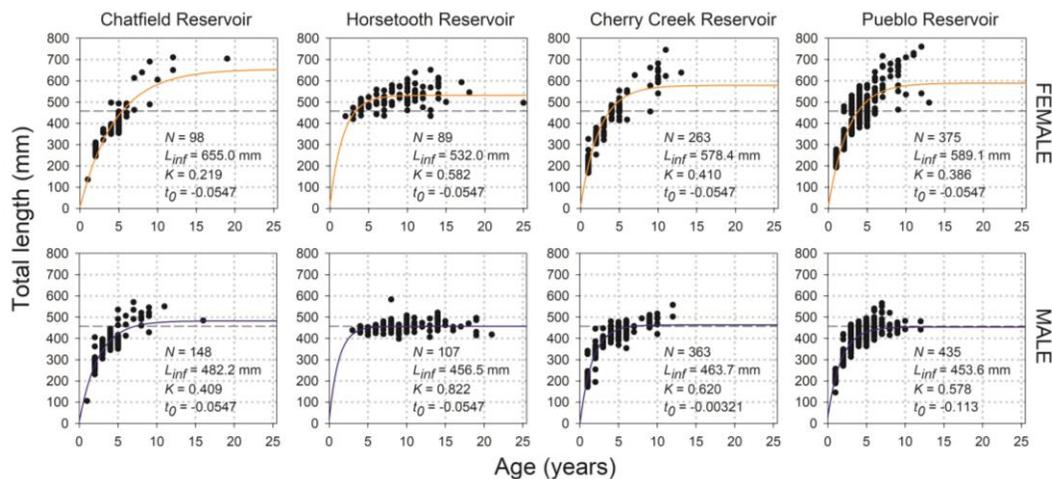

Figure 4. Length-at-age in spring estimated from sagittal otoliths (points; N = sample size) and corresponding von Bertalanffy growth functions (curves) and estimated parameters for female (top panels) and male (bottom panels) Walleye in four Colorado Reservoirs.

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RESEARCH PRIORITY: Informing triploid Walleye stocking procedures.

OBJECTIVES:

Evaluate risk associated with stocking Walleye with imperfect triploidy induction in systems void of diploids as a means for diversifying angling opportunities for anglers in sensitive locations.

INTRODUCTION:

The continued spread of nonnative species poses mounting and emerging challenges to fisheries managers. Introductions of predatory sport fish in particular, can undermine efforts to conserve native species (Tyus and Saunders 2000; Wolff et al. 2012) and disrupt existing food webs and fisheries (Hickley and Chare 2004; Eby et al. 2006; Johnson et al. 2017). Historically, introductions were largely intentional to provide food and recreation (Eby et al. 2006). New occurrences in unwanted locations now arise through natural dispersal or unauthorized stocking (Rahel 2000; Johnson et al. 2009). Because anglers exhibit high affinity toward predatory sport fish, manually suppressing these species for purposes of native fish protection or for maintaining existing fisheries may perpetuate conflict and illicit stocking in some areas. There is a need for management strategies that effectively reconcile these competing demands (Cowx et al. 2010).

Walleye *Sander vitreus* support valuable fisheries throughout their native range across the central-eastern United States and Canada (Colby et al. 1979; Schmalz et al. 2011). Given their popularity as a sport and food fish, Walleye were introduced to systems across western North America during the late 19th and early-mid 20th centuries (Billington and Sloss 2011). However, they represent a novel predator in these systems and can have detrimental effects on native species and salmonid fisheries that are common throughout the region (McMahon and Bennett 1996; Yule et al. 2000; Johnson et al. 2017). In addition, Walleye exhibit characteristics of successful invaders: large native range, wide environmental tolerance, high fecundity, predatory behavior, migratory capability, and human affinity (Ricciardi and Rasmussen 1998; McKinney and Lockwood 1999; Bozek et al. 2011). It is reasonable to expect Walleye to expand to new unwanted locations through natural dispersal or illegal stocking. Indeed, their range has grown and they represent an emerging threat in some high-profile locations across the western United States (McMahon and Bennett 1996; Bouwens et al. 2019; Hansen et al. 2019). Managers need an effective approach for discouraging future illegal introductions and suppressing existing populations in sensitive locations in a way that satisfies angler desire for Walleye fisheries.

The production and stocking of sterile triploid fish is a common fisheries management practice. Triploid fish are created by exposing eggs to hydrostatic pressure or other treatments (i.e., heat or chemical) post-fertilization which prevents extrusion of the second polar body (Fetherman et al. 2015). The result is an extra set of chromosomes (triploidy instead of diploidy) and putative sterility because synapsis is disrupted during meiosis which results in germ cells with chromosomal abnormalities (Thorgaard 1983; Strickberger 1985). Stocking sterile fish is advantageous for biological control of undesirable species (Winters et al. 2017) or for enhancing sport fisheries where preserving the genetic integrity of wild congeners is important (Kozfkay et al. 2006; Koch et al. 2018). In addition, triploids won't establish new populations if moved to other

waters. Lastly, stocking triploids or 'supermales' (i.e., YY fish) could suppress invasive populations by interfering with reproduction (Teem and Gutierrez 2010; Thresher et al. 2014; Schill et al. 2017). Despite dysfunctional meiosis, triploid males develop gonads and functional spermatozoa in aquaculture settings, but diploid eggs die after fertilization (Piferrer et al. 2009; Benfy 2011). If triploid males stocked into the wild exhibit gonadal development and or functional spawning behavior (i.e., entice diploid females to release eggs regardless of potential fertilization), effective reproductive interference and suppression of invasive populations is possible (Warrillow et al. 1997; Thresher et al. 2013).

Stocking sterile triploids could limit unwanted diploid Walleye and reduce angler motivation to transplant fish. Yet, little is known about the post-stocking performance of triploid vs. natural-origin diploid Walleye nor if triploids interfere with reproduction. In addition, the appropriate use of triploids depends on a number of biological factors. For example, attempting to swamp out the males of an unwanted diploid population may be less appropriate than other suppression methods if added predation from triploids reduces the integrity of a self-sustaining salmonid fishery (Johnson et al. 2017). Conversely, added predation may be acceptable where salmonids are supported through stocking (Yule et al. 2000), especially if diploids could disperse and threaten systems downstream (Horn et al. 2009; Bouwens et al. 2019). Starting new triploid populations in strategic locations void of diploids could reduce motivation to transplant fish.

Under current protocols, the triploidy induction rate (IR; mean proportion of fry that become triploid) for Walleye is generally high (>90%), but 100% is rare (Fetherman et al. 2015). Thus, developing and sustaining a new triploid fishery would require stocking fish with IR <100%, which poses a risk of starting a new feral population if the corresponding diploid fraction survives to maturity and produces successful progeny regularly. However, a host of biotic and abiotic factors influence natural recruitment in Walleye, which is often variable and sometimes fails (Hansen et al. 1998; Fetherman et al. 2015; Hansen et al. 2015; Koch et al. 2018). Targeting systems with attributes that generally limit natural recruitment should favor triploids. Further, unlike attempting to swamp an existing population, diploids would be outnumbered from the onset of stocking. Under this scenario, moderate levels of reproductive interference by triploid males may be sufficient to limit expansion of diploids above baseline levels. Therefore, developing new triploid Walleye fisheries in strategic locations void of diploids should not be immediately dismissed as a viable management strategy, but requires investigation.

The goal of this study was to explore the potential consequences of stocking Walleye with imperfect triploidy induction in locations void of diploids as a means for managing angler desire for Walleye fisheries proactively rather than reactively and in a way that is compatible with native species conservation or other fisheries management objectives. Specifically, we developed a joint stochastic age-structured model to characterize the population dynamics of triploid and diploid Walleye in hypothetical systems stocked with fingerlings at varying IRs <100%. We used the model to estimate the density of adult triploid vs. diploid Walleye and the probability of diploid persistence over a defined interval after ceasing stocking of triploids. In addition to varying IR, we simulated the effects of alternative (1) fingerling stocking rates and frequencies (e.g., every year vs. every-other-year); (2) reproductive interference scenarios (i.e., all mature triploid males vs. only a subset effectively participate in spawning); and (3) natural recruitment scenarios (e.g.,

variable and frequent vs. variable and infrequent). Collectively, these simulations enabled discrimination of how different stocking strategies affect the tradeoff between triploid Walleye fishery quality and potential diploid productivity and associated dependencies on key biological processes.

METHODS:

Study region.—We tailored the modelling analysis to reflect fisheries management and ecological constraints facing reservoirs within the upper Colorado River Basin (UCRB), USA, as this region is at the forefront of issues concerning native fish protection and angler desire for nonnative predatory sport fish (Hansen et al. 2019). The upper Colorado River contains critical habitat for the endemic Colorado Pikeminnow *Ptychocheilus lucius*, Humpback Chub *Gila cypha*, Bonytail *G. elegans*, and Razorback Sucker *Xyrauchen texanus.* The basin is heavily impounded, and most reservoirs contain nonnative piscivores (e.g., Smallmouth Bass *Micropterus dolomieu* and Northern Pike *Esox lucius*) that have dispersed and established self-reproducing populations within portions of critical habitat for endangered fish downstream (e.g., Zelasko et al. 2016). Although some of these reservoir introductions were once authorized, the majority occurred through unauthorized means, which is now a major fisheries management issue facing the region (Johnson et al. 2009).

Reservoir fisheries management in the UCRB, particularly in the state of Colorado, emphasizes a suite of measures that attempt to reconcile nonnative sport fishing with native fish protection. These include (1) stocking nonnative salmonids because of their limited effects on native fish downstream and limited ability to reproduce naturally in the basins reservoirs (Hansen et al. 2019); (2) implementing harvest incentive programs to involve anglers more directly in the management/suppression of nonnative piscivores in sensitive locations (Hansen 2018); and (3) constructing anti-escapement devices (e.g., outlet screens or block-nets for spillways) to limit downstream dispersal from known source populations (e.g., Breton et al. 2013). With an anti-escapement device in place, some nonnative cool- (e.g., tiger muskie *Esox masquinongy × Esox lucius*) or warm-water (e.g., Largemouth Bass *Micropterus salmoides*) piscivores deemed compatible with native fish protection can be managed through stocking (Martinez et al. 2014). This includes triploid Walleye, but stocking has been inhibited by ongoing debate regarding the appropriateness of releasing fish with IRs <100%.

Overall management and stocking scheme.—We modeled population dynamics over a time-frame relevant to fisheries managers and the expected average life-span of Walleye in Colorado (20 years; A. G. Hansen, unpublished data). Each simulation was 40 years. Within the model, triploid Walleye fingerlings were stocked at different rates, frequencies and IRs for the first 20 years ('triploid stocking phase'), then stocking ceased. Diploid density (of both stocked- and natural-origin) and persistence were tracked for the following 20 years ('diploid persistence phase') as triploids waned from the system through natural and fishing mortality. We then asked whether a 'viable' diploid population (defined below) remained at year 40 (Figure 1). If so, then diploids of natural-origin could continue to persist fully free of potential triploid influence—an undesirable long-term consequence of a new stocking program.
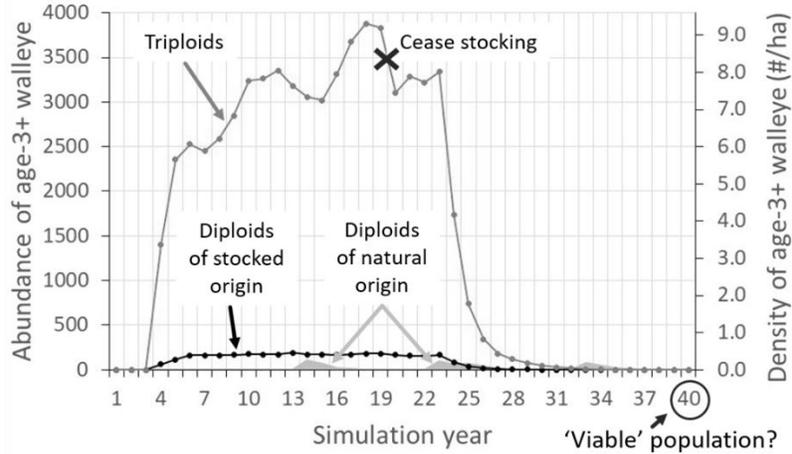
Figure 1. Example model simulation demonstrating the overall management and stocking scheme. For the scenario portrayed here, 25,000 walleye fingerlings were stocked annually with a triploidy induction rate of 95%. In addition, this simulation assumed no reproductive interference by mature triploid male Walleye. Density was computed using the average surface area of three Colorado reservoirs (272 ha when each at full pool) currently stocked or proposed for triploid walleye management.

Standardizing the time-frame to the life-span of Walleye offered an objective and cautious approach to evaluating the potential consequences of stocking triploids with imperfect induction. This scheme (1) enabled full manifestation of short-term population dynamics in the model as most or all expected age-classes could be present in the system; (2) measured persistence at a stage when diploids of stocked-origin would be absent and no longer contribute to potential reproduction, perhaps making it more difficult for diploids of natural-origin to persist further; and (3) eliminated the possibility of underestimating the probability of persistence simply through giving the diploid populations more opportunity to collapse by prolonging stochastic simulations over a time-frame irrelevant to decision makers. Preliminary model exploration demonstrated greater levels of population collapse when extending the duration of simulations beyond that defined here, which would lead to less conservative recommendations.

Age-structured model.—Age (a; max age = 20), sex ($\male$, $\female$), and year-specific (i) abundance ($N_{a,i,\male\ or\ \female}$) of catchable-sized (age 3+) triploid Walleye of stocked-origin and diploid Walleye of stocked- and of natural-origin were tracked separately (referred to as 'groups'), but simulated in tandem, based on age- and sex-specific annual survival rates ($s_{a,\male\ or\ \female}$; proportion from 0-1) that subsumed both natural and fishing mortality:

$N_{a,i+1,\male\ or\ \female} = N_{a,i,\male\ or\ \female} \cdot s_{a,\male\ or\ \female}$, where $a \geq 3$ to 20 for each group.

The number of fingerlings (FINGs) released in spring, their IR (proportion from 0-1) and sex-ratio (always $1\male$:$1\female$) determined the number of age 0 male and female triploids and diploids of stocked-origin (denoted by n) entering the system each year stocking occurred:

$n_{triploid,i,\male\ or\ \female} = (\text{FINGs} \cdot \text{IR})/2$,

$n_{diploid,i,\male\ or\ \female} = [\text{FINGs} \cdot (1 — \text{IR})]/2$.

The corresponding number of age 0 diploid fingerlings of natural-origin (denoted by R) was treated as a density-dependent function of spring spawner abundance (S; males and females of mature age combined) using a Ricker stock-recruitment model (Ricker 1975):

$$R_i = \alpha S_i e^{-\beta S} e^{\varepsilon},$$

where α represents the maximum expected recruits per spawner, β regulates the strength of density-dependence, and e^{ε} [$\varepsilon \sim N(\mu = 0, \sigma > 0)$] recreates lognormal deviates around the underlying deterministic relationship to simulate annual variation in recruitment. Lastly, mortality over the first three years of life was integrated into a single survival rate (s_{0-3}; proportion from 0-1) to compute the starting abundance of catchable, age 3 individuals for each group and cohort.

It is possible that male triploid Walleye of mature age interfere with diploid reproduction. Therefore, we adjusted S_i and computed the number of 'effective' diploid spawners (ES_i) based on the relative number of mature diploid males ($M_{diploid,i}$) vs. mature triploid males ($M_{triploid,i}$) that successfully participate in spawning each year before computing R_i:

$$ES_i = S_i \cdot \frac{M_{diploid,i}}{[M_{diploid,i} + (M_{triploid,i} \cdot p)]},$$

where p is the proportion of mature triploid males that successfully participate. Thus, if no participation occurs (i.e., $p = 0.0$), then $ES_i = S_i$. Adjusting S_i in this way assumed random mating wherein the probability of a diploid female spawning with a triploid male was simply the fraction of all mature males present that are triploid. The parameter p in essence equates to what has been interpreted as a 'fitness' factor in other studies simulating the effects of stocking male fish with chromosomal abnormalities (e.g., YY supermales) on the suppression of existing invasive populations (Senior et al. 2013; Schill et al. 2017). Here, if only 25% ($p = 0.25$) of mature triploid males successfully participate in spawning, then collectively, they are only 1/4th as reproductively fit as their wild diploid counterparts.

Model parameterization.—The model was parameterized using field data and literature values. Values for $s_{a,\male \; or \; \female}$ (40-66% depending on age) were estimated using catch-at-age from diploid Walleye in Pueblo Reservoir. Pueblo Reservoir represents one of Colorado's Walleye broodstocks which is supported through annual stocking. Restrictive harvest regulations protect the broodstock, so should yield relatively high estimates of $s_{a,\male \; or \; \female}$ (Blackwell et al. 2020). We sampled the reservoir during 2018 following the standardized Fall Walleye Index Netting procedure (FWIN; Giacomini et al. 2020). Two readers aged sagittal otoliths from a systematic random subsample of fish captured and these data were used to construct sex-specific age-length-keys (Isley and Gabrowski 2007). Length-frequency data from the FWIN survey were adjusted for size-dependent gill-net retention following the methods of Hansen (2019) prior to application of age-length-keys to generate minimally-biased estimates of catch-at-age. Weighted catch-curve regression was then used to estimate $s_{a,\male \; or \; \female}$ for different age-groups of fish (Slipke and Maceina 2010). Because FWIN catch of larger, older (>age 10) Walleye was relatively low, we used length-frequency data of mature fish captured in multifilament-nylon single-mesh gill nets during spring spawning operations for the analyses described above. For the manuscript in preparation, we will likely

include $s_{a,\male \text{ or } \female}$ values estimated from FWIN surveys on other stocked brood waters and Horsetooth Reservoir (natural reproduction only) to better characterize potential variation in these survival parameters.

Parameters for the Ricker stock-recruitment model (α, β and σ) were estimated from long-term survey data tracking the abundance of adult fish ≥age 5 (males and females combined) and the fall abundance of age 0 fish over the 1958-1996 period in Escanaba Lake, WI (Hansen et al. 1998). Age 5 was when the majority (~80%) of females reached sexual maturity (Serns 1982). We fit the stock-recruitment model to these data using maximum likelihood methods assuming lognormal error with the mle2 function from the bbmle package in R (Figure 2).
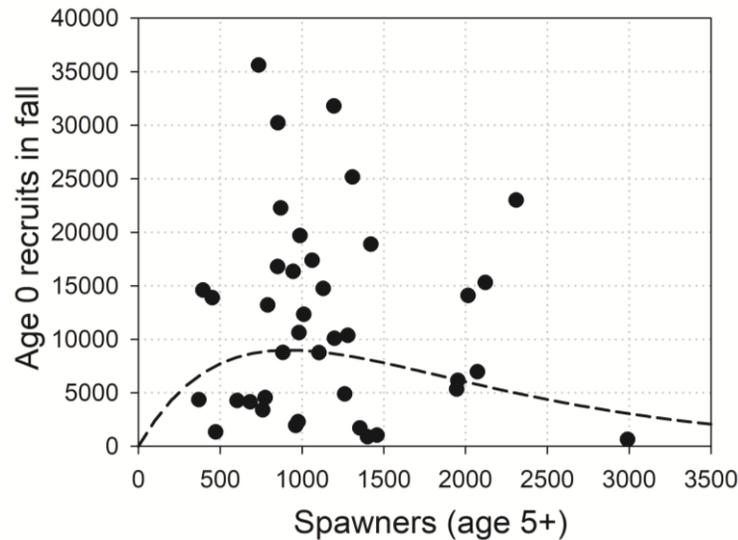

Figure 2. Fitted Ricker stock-recruitment model (line) to data (points) from Escanaba Lake, WI collected over the 1958-1996 period (Hansen et al. 1998). The resulting model equation was: $R = 26 \times S \times e^{(-0.001 \times S)} \times e^{[N(\mu = 0, \sigma = 1.008)]}$.

There is a positive association between adult Walleye density and lake surface area (Baccante and Colby 1996). Although small, Escanaba Lake (119 ha) best reflected the size and contained a similar sportfish community as reservoirs in the UCRB when compared to other populations with long-term spawner-recruit data. In addition, year-classes were detected each year over the 1958-1996 period—prior to declines in natural recruitment and increases in year-class failure observed more recently in the upper Midwestern USA (Hansen et al. 2015). Further, the mean fecundity estimated for female Walleye in Escanaba Lake exceeded that of 79% of other waters examined across North America (Baccante and Colby 1996). Thus, we felt data from Escanaba Lake would provide maximum expectations for the potential annual reproductive output and variability therein from a naturally reproducing diploid Walleye population in a small UCRB impoundment.

Estimates for overall survival from age 0 in fall to age 3 in spring (s_{0-3}) and corresponding interannual variation (mean = 12%, SD = 1.9%, N = 7 years) for natural-origin fish were also derived from the Escanaba Lake Walleye population. Because Walleye of stocked-origin exhibited reduced survival when compared to conspecifics of natural-origin in Escanaba Lake, we reduced mean s_{0-3} to 6.5% for the stocked triploid and diploid fingerlings in the simulation model. The magnitude of this reduction reflected differential survival estimated from the top performing

stocked cohorts (Kempinger and Churchill 1972). Further, triploid and diploid saugeyes (Walleye *Sander vitreus* × Sauger *S. canadensis*) stocked into Kansas reservoirs demonstrated that the relative survival of triploid fish was approximately half that of diploid fish (Koch et al. 2018). Although this information is not yet available for triploid Walleye, to remain conservative, we reduced s_{0-3} for the stocked triploid fingerlings by an additional 50%, resulting in a value that was approximately one quarter of that simulated for diploid fish of natural-origin.

Modifying stock-recruitment to reflect limited reservoir conditions.—When simulating the stock-recruitment model derived from Escanaba Lake, a measurable year-class of natural-origin fish was generated every year and was at or above average for a given spawner abundance in over 50% of years. Therefore, it provided baseline expectations for what a diploid Walleye population that recruits annually might look like in a reservoir where abiotic and biotic factors are not limiting. Alternatively, to simulate populations in systems where occasional year-class failure would be anticipated, we included an additional 'coin flip' using the binomial distribution to determine whether the number of age 0 fish predicted from the stock-recruitment model each simulation year would succeed or fail. The probability of success was weighted such that natural recruits survived to fall one-in-three or one-in-six years on average. These frequencies recreated the fragmented age-structure observed for gravid female Walleye sampled and aged with sagittal otoliths from Rifle Gap Reservoir, CO (145 ha impoundment within the UCRB) over 2017-2019 (C. J. Farrell, unpublished data). Although we have some empirical support for intermittent reproduction, standard fall surveys designed specifically for monitoring natural recruitment from introduced diploid Walleye in key UCRB reservoirs are needed to better inform dynamics and provide additional context for the general model scenarios explored here.

The age at which most females become sexually mature is another important consideration when modifying the stock-recruitment model for application to diploid Walleye inadvertently stocked into more ecologically constrained systems. Cumulative growing degree days based on air temperature (base value of 5°C) is a strong predictor of length and age at 50% maturity for Walleye over their native range (Baccante and Colby 1996; Venturelli et al. 2010a). However, regression models generated from these studies did not accurately predict maturity for some known reservoir populations in Colorado—perhaps due to differences in biophysical properties, prey conditions or other variables. So, we used empirical data from introduced diploid Walleye in Narraguinnep Reservoir (215 ha impoundment in the UCRB) to inform the age at which the majority of females become sexually mature (≥age 7; C. J. Farrell, unpublished data) to align with the selection of ≥age 5 in Escanaba Lake by Hansen et al. (1998).

Defining a 'viable' diploid Walleye population and acceptable risk thresholds.—We placed minor constraints on what constitutes a 'viable' diploid Walleye population. Early model exploration indicated that the argument of 'it only takes two' (reproductive individuals) was not sufficient for population persistence under the assumption of intermittent reproduction. Rather, having a mix of younger and older age-classes collectively was necessary for at least short-term persistence in the face of potential year-class failure. Therefore, two conditions were required at year 40 of each simulation to constitute a viable population: at least two non-reproductive diploid fish (one ♂ and one ♀) <age 7 and at least two reproductive diploid fish (one ♂ and one ♀) ≥age 7. For each combination of IR, stocking rate and frequency, reproductive interference and natural recruitment

scenarios, we simulated the model 10,000 times and tracked the number of occurrences in which conditions for a viable diploid population were achieved in order to compute the overall probability of diploid persistence (P_d = number occurrences/10,000). For purposes of summarizing results in an efficient manner, we assumed that $P_d \leq 0.05$ was an acceptable level of risk when considering starting a new triploid Walleye stocking program in a system void of diploids. However, decision makers should identify their own acceptable risk threshold when interpreting results from this study, as it likely depends on a number of system-specific physical (e.g., proximity and connectivity to sensitive native fish habitat), biological and social (e.g., regional need to diversify angling opportunities) factors.

Uncertainty in induction rate.—See Fetherman et al. (2015) for a detailed description of current induction rate testing and estimation procedures in the state of Colorado. We regressed the SD as a function of IR estimated from 21 independent lots of triploid Walleye fry produced by Colorado Parks and Wildlife over the 2018 and 2019 spawning years to characterize the average amount of uncertainty associated with each relevant level of IR for purposes of simulation modeling. Observed IRs and SDs ranged from 73-99% and 0.2-7%, respectively. As anticipated, SD declined as IR approached 100%, but no apparent downward trend was observed until IR exceeded 85%. Therefore, the same SD was applied to all IRs $\leq$85%. Because IR cannot exceed 100%, we used the truncated normal distribution to simulate uncertainty associated with the percent triploidy stocked each year at a given target IR level in the population model (Figure 3).
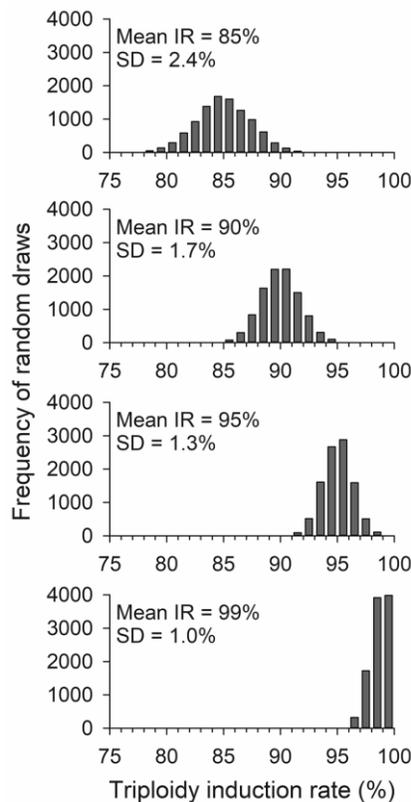

Figure 3. Frequency of 10,000 random draws from a truncated normal distribution with different means and SDs demonstrating the uncertainty associated with progressively increasing mean triploidy induction rate estimates derived from current sampling and testing procedures (see Fetherman et al. 2015).

RESULTS & **DISCUSSION**:

Rather than reporting results from all model scenarios examined, we focused on those most pertinent to Ridgway Reservoir (417 ha impoundment in UCRB) here, as this is the only reservoir currently being proposed by Colorado Parks and Wildlife for a new triploid Walleye stocking program. A rigid fish screen for the spillway to minimize escapement is pending. To keep faith with anglers and diversify fishing opportunities, mangers are looking to replace Smallmouth Bass—which are actively being suppressed through angler incentives—with a desirable predatory sportfish (triploid Walleye) more compatible with native fish conservation efforts downstream. However, if constrained by strict requirements on the minimum IR, stocking quotas may not be met in all years, which could compromise fishery quality as well as relationships with anglers.

Ridgway Reservoir is oligotrophic which could limit the feeding and growth of natural-origin fry. Greater size can positively influence the survival of stocked Walleye (Weber et al. 2020), and stocking relatively large fingerlings may be required to overcome potential early ecological bottlenecks if poor recruitment of triploids is observed. In addition, Ridgway Reservoir is typically in flux during periods that may be critical for natural reproduction. Irrigation releases generally begin mid-March before inflows ramp up which leads to declining water levels during potential spawning, egg incubation and early fry rearing periods for Walleye. Reservoir fluctuations can affect year-class strength in Walleye, but is only positively influenced when water levels are rising (Felts et al. 2020). Water levels are generally increasing during these same periods for Smallmouth Bass as inflows start to exceed outflows (Figure 3).
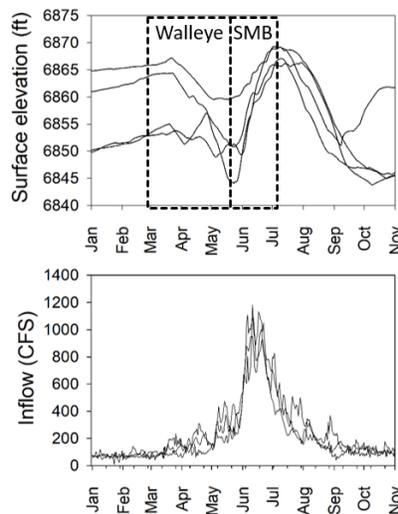

Figure 3. Ridgway Reservoir surface elevations and corresponding inflows for the 2017-2019 water years. Potential spawning, egg incubation and fry rearing periods based on observations from other reservoirs are bracketed for both Walleye and Smallmouth Bass.

Simulation modeling demonstrated non-linear patterns in P_d over the range of scenarios examined. For each scenario presented here, we assumed a stocking rate of 25,000 triploid fingerlings—the average number currently being stocked into two other UCRB reservoirs in Colorado with established diploid Walleye populations. We also assumed intermittent reproduction wherein diploid Walleye produced a successful year-class one-in-three or one-six-years on average.

First, assuming no reproductive interference from triploid males and intermittent reproduction wherein a successful diploid year-class of natural-origin was produced one-in-six years on average, IRs of ≥93% were required for P_d to remain below the acceptable risk threshold of 0.05 when stocking 25,000 fingerlings annually. Alternatively, IRs of ≥85% were required if 25% ($p = 0.25$) of triploid males successfully participated in spawning each year. Given the strong effect of having only moderate reproductive interference, reducing s_{0-3} for triploid fingerlings by an additional 50% relative to the stocked diploids did not change the outlook notably for IRs ≥90% (Figure 4).
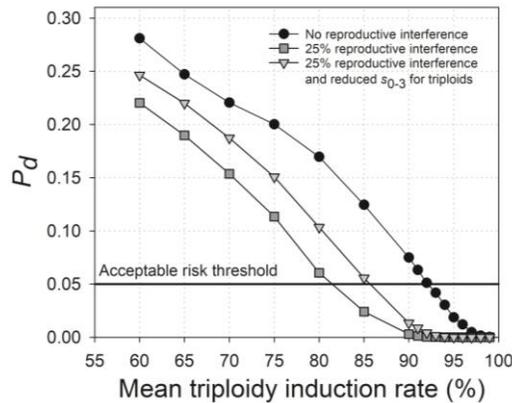
Figure 4. Probability of diploid persistence (P_d) as a function of the mean triploidy induction rate of 25,000 triploid Walleye fingerlings stocked annually. Simulations assumed different levels of reproductive interference by triploid males and reduced early survival of triploid fingerlings from age 0 in fall to age 3 in spring (s_{0-3}). These simulations also assumed intermittent reproduction from diploid Walleye wherein a successful year-class was produced one-in-six years on average.

Interestingly, stocking 25,000 triploid fingerlings every-other-year rather than annually reduced P_d to a similar extent as having moderate reproductive interference from triploid males. Including moderate reproductive inference accentuated the reductions in P_d associated with stocking less frequently, even when reducing s_{0-3} for triploid fingerlings by an additional 50% relative to the stocked diploids (Figure 5).
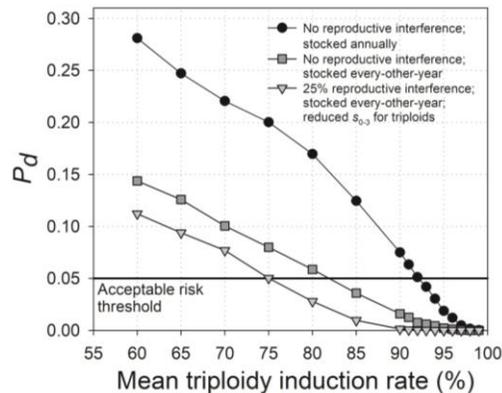

Figure 5. Probability of diploid persistence (P_d) as a function of the mean triploidy induction rate of 25,000 triploid Walleye fingerlings stocked annually versus every-other-year. Simulations assumed different levels of reproductive interference by triploid males and reduced early survival of triploid fingerlings from age 0 in fall to age 3 in spring (s_{0-3}). These simulations also assumed intermittent reproduction from diploid Walleye wherein a successful year-class was produced one-in-six years on average.

It is possible that diploid Walleye produce successful year-classes more frequently, despite *a priori* expectations for recruitment limitation based on the physical and biological attributes of reservoirs proposed for stocking. Values for P_d were elevated across the full range of IR when assuming year-classes were produced one-in-three rather than one-in-six years on average. However, moderate reproductive interference from triploid males or stocking every-other-year or both helped mitigate the elevated risk associated with more frequent natural recruitment from diploids. Under these scenarios, IRs of ≥95% were necessary for remaining near or below the acceptable risk threshold of 0.05. Although, when stocking annually with no reproductive interference, IRs of ≥98% were required to remain below the threshold (Figure 6).
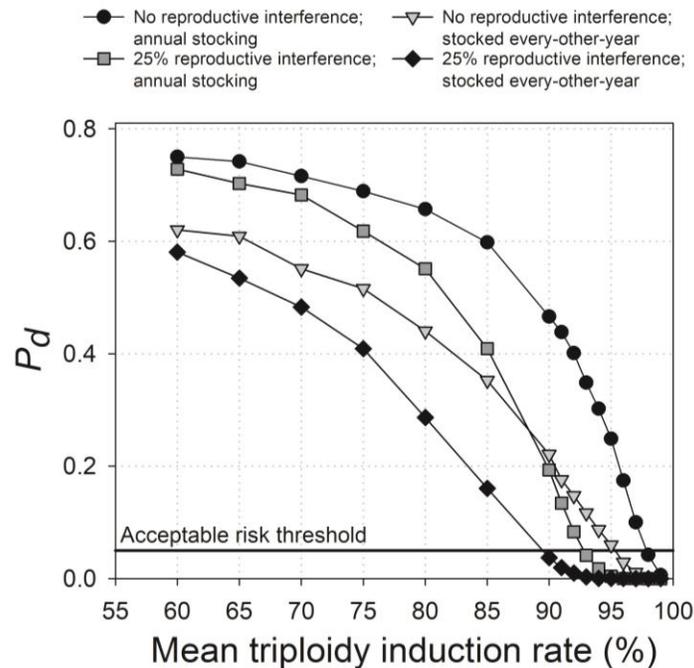

Figure 6. Probability of diploid persistence (P_d) as a function of the mean triploidy induction rate of 25,000 triploid Walleye fingerlings stocked annually versus every-other-year. Simulations assumed different levels of reproductive interference by triploid males. For all simulations, the early survival of triploid fingerlings from age 0 in fall to age 3 in spring was reduced by 50% relative to the stocked diploids. These simulations also assumed intermittent reproduction from diploid Walleye wherein a successful year-class was produced one-in-three years on average.

SUMMARY:

The simulation model was structured and parametrized to reflect potential recruitment dynamics of diploid Walleye in Colorado's unproductive, fluctuating reservoirs using the best information available. The model revealed novel insights that should be considered by managers before initiating a new triploid Walleye stocking program. Modest spawning participation by triploid males and reduced stocking frequency had strong and comparable effects on risk. Both flattened the curve across the 90-99% IR range at a stocking rate of 25,000 fingerlings—even when the early survival of triploids was reduced by half compared to diploids. Thus, stocking every-other-year represents a cautious approach to developing a new triploid Walleye fishery amidst lingering uncertainties regarding whether and how much males interfere with reproduction and the frequency of natural reproduction in the system.

The model demonstrated some capacity to adjust the fingerling stocking rate and frequency to optimize the tradeoff between triploid Walleye fishery quality (density of catchable-sized fish) and risk of diploid persistence at a given target IR. By stocking annually, model predicted densities of catchable-sized (≥age 3) triploid Walleye peaked near the median (14.8 adults/ha) observed from 85 diploid populations across North America (Baccante and Colby 1996). Thus, developing a triploid fishery of reasonable quality seems possible even at a relatively low stocking rate (given the average size of UCRB reservoirs), which should help reduce risk of diploid persistence. As expected, peak densities were reduced by approximately half when stocking every-other-year rather than annually. However, bumping the stocking rate to 50,000 fingerlings helped maintain higher peak densities while also taking advantage of the reduced risk associated with stocking less frequently. Conversely, assuming intermittent reproduction (year-class one-in-six years) and stocking at ≥95% triploidy, diploid populations bumped along at low peak densities of <0.85 catchable fish/ha on average with occasional short-term (few years) increases to 2.5 catchable fish/ha (stocked and natural-origin fish combined) over both the 'triploid stocking' and 'diploid persistence' phases of the model. These low predicted densities highlighted the importance of stocking for maintaining fisheries in ecologically constrained systems.

The largest, oldest female Walleye in exploited populations may contribute most to natural recruitment through high fecundity and maternal effects which can govern population dynamics. For example, the maximum reproductive rate of Walleye in Lake Erie was approximately two-fold higher when older females were abundant vs. when they were relatively scarce (Venturelli et al. 2010b). In addition, over the 1958-1996 period, the abundance of age 5+ spawners (males and females combined), density of Yellow Perch *Perca flavescens* and variation in May surface temperatures explained 89% of the variation in the fall abundance of age 0 Walleye in Escanaba Lake (Hansen et al. 1998). However, these same variables explained little to no variation when extending the time-series through 2015. Metrics related to egg production from the largest (>55.9 cm), oldest (≥age 10) females explained the most variation (Shaw et al. 2018). In addition, the maternal age and body condition of Walleye has been positively linked to egg quality, hatching success and offspring quality (Moodie et al. 1989; Johnston 1997; Johnston et al. 2007; Venturelli et al. 2010b). In ecologically constrained systems, we might anticipate maternal effects to be particularly important in driving natural recruitment. In this context, modifying the stock-recruitment model from Escanaba Lake by increasing the age at which the majority of females are mature to age 7 rather than age 5 was still conservative.

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RESEARCH COMMUNICATION AND TECHNICAL ASSISTANCE

Reporting period: May 2018 – November 2020.

Peer-reviewed Publications:

- **Hansen, A. G.** 2019. Size-dependent retention of pelagic-oriented kokanee in multimesh gill nets. *North American Journal of Fisheries Management* 39:921-932.

- **Hansen, A. G.**, J. S. Thompson, L. N. Hargis, D. Brauch, and B. M. Johnson. 2019. Predatory threat of introduced Yellow Perch in a salmonid dominated reservoir food web. *North American Journal of Fisheries Management* 39:172-190.

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External Presentations:

- **Hansen, A. G.**, C. J. Farrell, and B. M. Johnson. Simulated effects of triploid Walleye induction rate on diploid persistence in a newly stocked population. Biology Committee Webinar, Upper Colorado River Endangered Fish Recovery Program. September 3rd, 2020.

- Farrell, C. J., **A. G. Hansen**, B. M. Johnson, and C. M. Myrick. Does ploidy affect mercury bioaccumulation in Walleye? American Fisheries Society, Virtual Annual Meeting. September 2020.

- Farrell, C. J., B. M. Johnson, C. A. Myrick, **A. G. Hansen**, M. M. Brandt, and J. White. A preliminary assessment of adult diploid and triploid Walleye in Narraguinnep Reservoir, Colorado. Annual CO-WY AFS Meeting, Laramie, WY. February 25th, 2020. **Voted best student paper**.

- **Hansen, A. G.**, E. I. Gardunio, and T. Eyre. Population dynamics of Smallmouth Bass in two upper Colorado River Basin reservoirs: short-term responses to an angler incentive program. UCRB Researcher's Meeting, Durango, CO. January 14th, 2020.

- **Hansen, A. G.**, and D. A. Beauchamp. Pelagic food web interactions in Lake Tahoe: considerations for the reintroduction of Lahontan Cutthroat Trout. Joint AFS-TWS meeting, Reno, NV. October 3rd, 2019.

- Farrell, C., B. M. Johnson, C. M. Myrick, **A. G. Hansen**, M. Brandt, and J. White. Induced triploidy for managing invasive Walleye: study overview and preliminary findings. Annual

meeting of CO-WY Chapter of the American Fisheries Society. February 28th, 2019. Fort Collins, CO.

Internal Presentations:

- **Hansen, A. G.** How low can we go? Simulated effects of triploid Walleye induction rate on the probability (risk) of diploid persistence in a newly stocked population. Virtual meeting among representatives of CO, UT, and the USFWS. March 23rd, 2020.

- Brauch, D., and **A. G. Hansen**. Blue Mesa Lake Trout management update. Biologist Meeting, Evergreen, CO. January 22nd, 2020.

- **Hansen, A. G.**, and D. Brauch. Population dynamics of Lake Trout in Blue Mesa Reservoir: new insights from confronting simple models with long-term survey data. Biologist Meeting, Evergreen, CO. January 22nd, 2020.

- Farrell, C. J., B. M. Johnson, C. A. Myrick, **A. G. Hansen**, M. M. Brandt, and J. White. Induced triploidy for managing invasive Walleye: study overview and preliminary findings. Biologist Meeting, Evergreen, CO. January 22nd, 2020.

- **Hansen, A. G.**, B. M. Johnson, and C. J. Farrell. How low can we go? Simulated effects of triploid Walleye induction rate on the probability of establishing a new diploid population. Senior Staff Meeting, Brush, CO. December 10, 2019.

- Farrell, C. J., B. M. Johnson, C. A. Myrick, **A. G. Hansen**, M. M. Brandt, and J. White. Induced triploidy for managing invasive Walleye: study overview and preliminary findings. Senior Staff Meeting, Brush, CO. December 10, 2019.

- **Hansen, A. G.**, and C. Tucker. Integrating angler dynamics and Walleye biology to explore alternative harvest strategies for brood stock in Pueblo Reservoir. 2019 Biologist Meeting. January 24, 2019. Salida, CO.

- **Hansen, A. G.**, and D. Brauch. Assessing emerging threats to kokanee in Blue Mesa Reservoir: illegally introduced Yellow Perch and gill lice. Coldwater Reservoir Management Meeting, Buena Vista, Colorado. March 3rd, 2019.

Other Research Communication & Technical Assistance:

- Associate Editor for North American Journal of Fisheries Management (April 2019 – present).

- Anonymous peer reviewer for: Ecology and Evolution (1 manuscript); Environmental Biology of Fishes (1 manuscript); Fish and Fisheries (1 manuscript); Fisheries (2 manuscripts); Journal of the American Association for Laboratory Animal Science (1 manuscript); North American Journal of Fisheries Management (1 manuscript); Plos One (1 manuscript); Scientific Reports

(Nature Research Group; 1 manuscript); Transactions of the American Fisheries Society (2 manuscripts).

- CPW Fact Sheets: 'Lake Trout Population Monitoring' and 'Predation on Stocked Fish'.

- Farrell, C, B. M. Johnson, C. A. Myrick, and **A. G. Hansen**. Triploid Walleye: a new frontier for managing coolwater predators in the West. Progress Report. September 3, 2019. 86 pages.

- Treble, A. J., and **A. G. Hansen**. 2019. Hydroacoustics-based estimates of Rainbow Smelt (*Osmerus mordax*) abundance in Horsetooth Reservoir: 2017-2019. CPW Aquatic Research Summary Report. 8 pages.

- Fishes of Colorado contributed book chapters: 'Rainbow Smelt' and 'Tiger Trout'.

News, Stories and Interviews:

- Research on harvest management of Walleye in Colorado highlighted in a story written by Dan England. Title: *Managing Walleye: One Minor Change Can Have a Big Impact*. Colorado Outdoors Magazine, July 2020 Fishing Guide, No. 29.

- CPW News Release (11/15/2019) prepared by Jason Clay, NE Region PIO, titled: *CPW launches Walleye study to assess population dynamics at Lake Pueblo, Chatfield, and Cherry Creek*.

- FOX 31 local news story on Chatfield Reservoir Walleye study. Title: *CPW Conducts Aquatic Research Despite Single-Digit Temperatures*, by Ashley Michels. Aired October 30th, 2019. Link: https://kdvr.com/2019/10/30/cpw-conducts-aquatic-research-despite-single-digit-temperatures/

- CBS 4 local news story on Chatfield Reservoir Walleye study. Title: *Wildlife Scientists Research Colorado Walleye in Sunshine or Winter Weather*, by Conor McCue. Aired October 30th, 2019. Link: https://denver.cbslocal.com/2019/10/30/colorado-parks-wildlife-walleye-scientists/

- Interviewed by Wilbur Flachman for short story on fall turnover in high mountain lakes. Title: *True tales from the lying log*. Thirst Colorado, September/October 2019, Vol. 4, No. 6.

- Interviewed by Geoff Mueller, Senior Editor, The Drake Magazine, for a short primer in the summer 2018 issue on Tiger Trout and tiger muskie research, management, and angling opportunities. May 15th, 2018. Article was titled *Going on safari: a tail of two tigers*.

- Research pertaining to biological effectiveness of incentive-based fishing tournaments for suppressing invasive Smallmouth Bass highlighted in a story written by Dan England titled *Bucket Biology* in Colorado Outdoors Magazine, May/June 2018, Vol. 67, No. 3.