Lake and Reservoir Research

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TABLE OF CONTENTS

LAKE AND RESERVOIR RESEARCH

Period covered: December 2024 – November 2025.

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 essential populations of fish; (2) use this information to identify and evaluate alternative approaches for enhancing 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:	**Opossum Shrimp investigations:** Evaluating the potential for reducing non-native Opossum Shrimp *Mysis diluviana* (hereafter 'Mysis') to restore *Daphnia* and improve water clarity in Grand Lake, Colorado.

OBJECTIVES

The overarching objective of this priority is to provide information that will guide management efforts to improve water clarity of Grand Lake, Colorado through the reduction of its non-native Mysis population. The specific objectives include: I) understanding the role of Mysis in the Grand Lake food web, II) assessing how removal of Mysis will affect water clarity in experimental settings, and III) analyzing the feasibility of removal efforts of Mysis at the whole lake-scale.

INTRODUCTION

The Grand Lake ecosystem has been impacted by its inclusion in an inter-basin water project and the addition of non-native species. In the mid-1900s, Grand Lake was incorporated into the US Bureau of Reclamation (USBOR) owned Colorado-Big Thompson (C-BT) Project that collects water from the Colorado River's headwaters and directs it to Colorado's Front Range and Eastern Plains. Water movement through Grand Lake by the C-BT project can impact water clarity, especially by the introduction of organic particles (McCutchan 2015). To mimic conditions prior to the incorporation into the C-BT Project, the Colorado Water Quality Control Commission set a water clarity standard for Grand Lake to maintain a mean Secchi depth of 3.8 m or more from July 1st to September 11th with a 2.5 m daily minimum. From 1969-1971, non-native Mysis were introduced into Grand Lake and other lakes in the region as a potential food source for Lake Trout *Salvelinus namaycush* and kokanee *Oncorhynchus nerka* (Silver et al. 2021). Mysis preferentially consume large-bodied zooplankton, especially filter-feeding *Daphnia* (Chipps and Bennett 2000), and Mysis in Grand Lake have functionally depleted *Daphnia*

(Johnson and Pate 2014). *Daphnia* are known to promote water clarity (Lampert et al. 1986), and their absence could be contributing to low water clarity in Grand Lake. Operational changes to the timing and delivery of water via the C-BT system by USBOR and its managing partners have shown improvements in water clarity, but the potential to reduce Mysis and improve water clarity further remains unclear.

Mysis are highly adaptable to a range of environmental conditions due to their flexible vertical migrations, generalist feeding habits, and adaptable life history. Mysis undergo daily vertical migrations, foraging near the surface during the night and returning to the bottom during daylight (Walsh et al. 2012). However, there is growing evidence that their migrations are partial, with only part of the population migrating at any given time (Euclide et al. 2017). Near the surface, Mysis predominantly eat zooplankton, whereas when Mysis are associated with the bottom, they typically eat detritus, other invertebrates, and even larval fish (Walsh et al. 2012; Bess et al. 2021). Mysis often rely on food from both benthic and pelagic habitats to sustain their populations (Johnson and Pate 2014; Stockwell et al. 2020). Their diverse diet allows Mysis to adapt to changes in the availability of food, making them resilient to changes in ecosystems that might negatively affect other organisms without the same capacity to adapt (Walsh et al. 2012). By moving to the bottom of the lake during daylight, Mysis also avoid pelagic and diurnal foraging fish, such as larger Lake Trout, which are abundant in Grand Lake (Walsh et al. 2012; Johnson and Pate 2014). Finally, Mysis can adjust their reproduction based on food availability and risk of predation by fish. When conditions are favorable for Mysis to grow rapidly, they can reproduce every year, but during unfavorable conditions, they can delay their reproduction for upwards of 3-4 years (Walsh et al. 2012). Mysis adaptability makes them effective at disrupting lake food webs but also makes their effects in any specific lake challenging to predict.

Mysis have been introduced to numerous lakes throughout North America, providing case studies to evaluate their impact and potential management options. Though Mysis were initially introduced to benefit sport fish productivity, the most common outcome has been disruption of recreational fisheries and plankton communities. Non-native Mysis have negatively affected fisheries, especially kokanee fisheries, by competing with fish over zooplankton throughout North America (e.g., Fredrickson 2017; Johnson et al. 2018; Silver et al. 2021; Tahoe Environmental Research Center 2021). In many cases, Mysis have suppressed *Daphnia* and degraded water clarity. Despite the disruption to fisheries and water clarity, reducing Mysis has only been researched and attempted in two cases to our knowledge, Lake Tahoe and Lake Okanagan. At Lake Tahoe, California, a plan for sustainable harvest of Mysis was established to control their abundance in Emerald Bay, and potentially Lake Tahoe proper (Tahoe Environmental Research Center 2021). At Lake Okanagan, British Columbia, Canada, the largest effort to remove Mysis from a reservoir has been underway for nearly 20 years (Andrusak et al. 2010). Although this effort has not been successful in reducing Mysis and restoring zooplankton (Schindler et al. 2012), it serves as a model which has helped establish the equipment requirements and methods needed to optimize Mysis harvest efforts. Grand Lake is unique in being deep enough to support Mysis but with an area small enough that reducing the numbers of Mysis is more likely feasible. Thus, investigating management options for Mysis at Grand Lake provides an opportunity to both improve water clarity for local communities and to evaluate the feasibility of such efforts for lakes and reservoirs where Mysis have invaded.

Our objective is to investigate the feasibility and effectiveness of reducing Mysis at Grand Lake to improve water clarity. Our investigation will be completed in three phases: I) lake sampling to understand the ecological roles of Mysis, II) laboratory and field experiments to test how removal of Mysis will affect water clarity in a controlled setting, and III) planning and evaluation of lake-scale Mysis control efforts. Expected outcomes include information to guide a management plan, scientific publications on lake ecology, communication of findings with local stakeholders, and training of early-career scientists. Partners on the project include Colorado State University, Colorado Parks and Wildlife, Northern Water, Three Lakes Technical Committee, the Three Lakes Watershed Association, and USBOR.

METHODS

The study includes three phases. Phase I began in summer 2025 with the support of project partners. Phase II will involve experiments to evaluate how reducing Mysis populations will affect water clarity in a controlled setting. Phase III will involve feasibility analysis of a Mysis reduction plan that is informed by the first two phases.

Phase I – Understanding the Role of Mysis in the Grand Lake Food Web: Phase I has involved literature review, analysis of historical limnology data, Mysis and fish population surveys, and collections of stable isotope samples (carbon and nitrogen) for food web analyses. Our aim in Phase 1 is to use observational field data to examine the role of Mysis as consumers and as prey for fish in the food web. In future analyses, these data will be combined with ongoing measurements of water chemistry, plankton, and water clarity by Northern Water (2025).

Between May and October 2025, we collected monthly samples of pelagic and benthic Mysis for density and stable isotope analysis at the sample locations established by Johnson and Pate (2013; Figure 1). Additionally, we divided the lake into three zones representing the east, middle, and west parts of the lake (Figure 1). Vertical net tows (described below) were taken to estimate Mysis pelagic densities at each of the eight original sample stations, while a benthic sledge was towed (described below) to estimate Mysis densities on the bottom in each of the three newly designated zones. Our sampling generally adhered to the Colorado Parks and Wildlife standardized procedure (Martinez et al. 2010). We collected Mysis samples during the full moon of each month. Mysis samples were collected for stable isotope analyses (frozen) and density estimates (stored in 70% ethanol), during both the night and the day. A 1 m diameter (0.785 m^2) net with 500 µm mesh was used to collect pelagic Mysis integrated throughout the water column. We deployed a benthic sledge (0.44 mm wide x 0.31 mm tall) with 500 µm mesh to sample the benthos, towing at an average speed of 2 km/h. We towed the sledge for 5 minutes in May, and 10 minutes for the remaining months. In the lab, samples were processed to estimate abundance and size structure of males, females, and juveniles. Brood counts were also conducted on the first 20 females encountered in nighttime samples from stations 2, 4, and 6 each month.

In August 2025, Lake Trout and other fish were sampled using the Summer Profundal Index Netting method (SPIN; Sandstrom and Lester 2009). As described in previous Coldwater Lake and Reservoir reports (e.g., Hansen et al. 2021), SPIN uses a suite 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] placed in random order) to capture Lake Trout in a way that allows one to estimate Lake Trout density directly (i.e., number per ha). These estimates are then scaled up to a total abundance based on the area of the lake or reservoir surveyed. Brown Trout *Salmo trutta* and White Suckers *Catostomus commersonii* were also collected during the surveys. Each fish was identified, measured (total and fork length, mm), and weighed (g), and a subset were sacrificed to collect otoliths, determine sex, weigh gonads, and assess gut contents.

At the same frequency and in the same three zones described above for Mysis benthic samples (Figure 1), we collected and froze periphyton, phytoplankton, zooplankton, Mysis, benthic invertebrates, and benthic detritus for stable isotope analysis. Fish tissue samples were also collected during the August SPIN survey. Periphyton was collected by scrubbing and rinsing rocks from the shore. The resulting slurry was pre-filtered through a 63 µm stainless steel sieve and then through a vacuum filter with pre-weighed and pre-combusted 47 mm glass fiber filters. Phytoplankton were collected by integrating water from the top 10 meters of the lake and filtering it through a 63 µm sieve. Then, to collect phytoplankton, the filtrate was filtered similarly to periphyton. Zooplankton were collected using a 64 µm mesh zooplankton net towed through the top 10 m. In the lab, zooplankton were sorted by size (> or < 500 µm) and, for the large partition, into cladocerans vs. copepods. Mysis were collected using the nighttime pelagic and benthic methods described above. In the lab, Mysis samples were processed to separate five females, five males, and 10 juveniles to be analyzed separately. Benthic invertebrates and detritus were collected using an Eckman grab. In the lab, benthic invertebrates were separated into oligochaetes, non-tanypod Chironomidae, and Isopoda. All isotope samples were dried for at least two days at 60°C and then ground. Samples were sent to the Cornell University Stable Isotope Laboratory for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ analyses.

Phase II - Experimental Effects of Mysis Reductions on Water Clarity: Organic and inorganic suspended particles decrease water clarity, and in Grand Lake, they are linked to pumping for the C-BT project and input from natural tributaries. Mysis are omnivorous and known to alter their feeding behavior based on available food and their size. The proposed management to remove Mysis assumes they are less effective at filtering out particles and algae than the native *Daphnia*, and that Mysis are currently limiting *Daphnia* in Grand Lake by consuming them. Phase II will test these assumptions to inform the efficacy of Mysis removal in Phase III.

Lab Experiments: Our goal is to compare the role of Mysis relative to native *Daphnia* in affecting water clarity in conditions that are representative of Grand Lake before and during summer pumping by the C-BT project. *Daphnia* represent the hypothesized dominant taxa after Mysis are reduced. These experiments will be conducted in aquaria (10 L) using water and plankton collected from Grand Lake, using methods modified from a similar experimental study with Lake Tahoe zooplankton communities (Bess et al. 2021). Response variables will include aspects of water quality (suspended solids, turbidity, organic matter, phytoplankton, nutrients) in relation to community composition (Mysis versus *Daphnia* dominated). We will also evaluate how Mysis size (juvenile vs adult) affects changes in clarity, as reduction of the Mysis population may alter their size structure. We have submitted a proposal to the USBOR to fund these experiments.

Field Experiments: Large in-lake mesocosm structures will be used to evaluate how reducing Mysis affects water clarity in Grand Lake through the hypothesized food web interactions described above. These experiments allow for more realism by allowing Mysis to undergo their daily migrations, incorporating the whole plankton community, and replicating natural lake conditions. Experimental treatments will have a 2x2 factorial design, manipulating Mysis density and nutrient (nitrogen and phosphorus) concentrations to evaluate the relative role of top-down vs bottom-up effects. Mysis densities will be altered to mimic potential Mysis reductions, and nutrients will be altered to represent the range of variation in concentrations introduced by CB-T pumping. All treatments will include *Daphnia* and the background plankton community. We will evaluate to what extent Mysis reductions facilitate *Daphnia* recovery across a range of nutrient concentrations and the resulting changes in water clarity. Response variables will include zooplankton, phytoplankton, and water chemistry and clarity. We submitted a proposal to the Windy Gap Fund to support these experiments.

Phase III – Feasibility Analysis for Mysis Removal: Phase I and Phase II will inform the plan for Mysis reduction, including feasibility and effectiveness at improving water clarity. Our plan will rely on trawl nets pulled by boats to remove Mysis, similar to efforts on Mysis-invaded Lake Tahoe and Lake Okanagan. The plan will include analyses of cost, timeline and effects of the removal effort on the local recreationists. Sonar surveys will determine where Mysis and fish are concentrated. This approach will minimize impacts on fish.

PROJECT PROGRESS

Phase I of our study is ongoing, and we have limited preliminary findings because the samples and data have just been collected. With extensive help from biologists at Colorado Parks and Wildlife, Northern Water, and members of Dan Preston's lab at Colorado State University, our group was able to complete comprehensive field sampling in 2025 of Mysis, fish, plankton, periphyton, detritus, and benthic invertebrates. With the results from these samples, we will be able to evaluate the role of Mysis in the Grand Lake food web, and indirectly, water clarity. From April to October, we worked approximately 700 person-hours in the field. Lab processing of samples has been ongoing and is expected to continue into the winter/early spring. By mid-winter, we expect to have preliminary findings regarding food web relationships in Grand Lake using stable isotope data. By late winter/early spring, we expect to have detailed findings on Mysis life history and food web characteristics. In total, the team worked approximately 400 person-hours in the lab.

With the results from Phase I, we will be prepared for a science-based approach to informing experiments that evaluate how reducing Mysis can promote zooplankton and improve water clarity in Grand Lake. These findings will directly inform the experiments we have proposed for Phase II. In turn, the combined findings from Phase I and II will inform science-based management goals and procedures for reducing Mysis to improve Grand Lake water clarity (Phase III).

RESULTS & DISCUSSION

Our preliminary results show that Mysis in Grand Lake are abundant and exhibit partial vertical migration. This suggests that they are having a strong impact on the lake food web and ecosystem, and that their behavior may play an important role in the effectiveness of future removal efforts. Mysis densities in 2025 were similar when compared to the previous survey in 2013, at approximately 800 individuals/m^2 during the month of June (Figure 2). Grand Lake continues to have among the highest densities of Mysis in the state (Silver et al. 2021). Pelagic Mysis were more abundant in the night surveys than the day surveys (Figure 3), while the opposite was true for benthic Mysis (Figure 4). Though there were fewer Mysis collected in the pelagic tows during the day (Figure 3), their densities remained relatively high, suggesting that a considerable portion of Mysis remain suspended off the bottom during the day (up to 1800 individuals/m^2 in some samples). These findings support growing evidence (Walsh et al. 2012; Bess et al. 2021) that Mysis populations can exhibit partial vertical migration between the benthic and pelagic habitats. Our preliminary findings suggest that depth and sex mediate Mysis partial migration in Grand Lake. Mysis exhibit stronger migration patterns (i.e., differences between day and night) at lower depths for both pelagic (Figure 5) and benthic (Figure 6) surveys. The sex ratio in both benthic and pelagic habitats varied between night and day and across months (Figure 7), and, with the exception of benthic surveys in June, the sex ratio tended to be skewed male.

The relatively high densities and partial vertical migration of Mysis in Grand Lake suggests that Mysis are broadly affecting the benthic and pelagic food webs in dynamic ways. Large-bodied zooplankton, the preferred prey of Mysis, are relatively rare in Grand Lake. As a result, Mysis appear to be leveraging their behavioral plasticity to feed benthically and throughout more of the water column (i.e., not just the surface). There is increasing evidence that Mysis rely on benthic foraging (O'Malley and Stockwell 2019; Stockwell 2020) and suspended organic particles (e.g., Bess et al. 2021). Given the lack of *Daphnia* and abundant suspended organic particles in Grand Lake, it is likely that Mysis are exhibiting similar feeding habits. We will explore this possibility using the results from our stable isotope results. Further, there may be consequences for the reproductive and production rate of the Mysis population in Grand Lake. Mysis brood count in Grand Lake tends to increase with female length (though not in a statistically significant way; Figure 8), and there is considerable variation in Mysis brood counts (especially in May: Figure 9). A median value of 10 embryos per brood is similar to what has been observed in oligotrophic systems like Lake Tahoe, but are low compared to more productive lakes (Beeton and Gannon 1991). When we finish processing our monthly density and population size structure estimates, we will be able to estimate Mysis growth rates and annual production. We will evaluate how their growth rates change by season, and how their growth may be enhanced by pumping activities. Further, we will be able to compare growth rates and annual production estimates to other lakes to further contextualize the role of Mysis in Grand Lake.

Our observation of partial vertical migration of Mysis in Grand Lake has consequences for our development of a Mysis management plan. If Mysis exhibit full vertical migration (i.e., all individuals migrate to the surface at night), then removal efforts using mid-water trawls could only be done at night. Our observation that a considerable portion of Mysis remain off the bottom during the day also means that they would be vulnerable to removal by mid-water trawling during both the night and the day, further increasing the feasibility of our proposal to reduce Mysis in Grand Lake. Colorado Parks and Wildlife also conducted preliminary hydroacoustic surveys of Mysis in fall 2025, which we will use to evaluate the depth and spatial variation in Mysis distribution across Grand Lake during the night and day.

Our fish surveys, using the SPIN protocol (reported in next section), suggest that Lake Trout and Brown Trout in Grand Lake have undergone changes since the 2013 investigation of the Grand Lake food web. We have not yet made comparisons of the fish population estimates between 2013 and 2025, but we have compared fish body condition using relative weight (Pope and Kruse 2007; Figure 10). Fish body condition was previously reported as relatively poor by Johnson and Pate (2014), however the condition of Lake Trout and especially Brown Trout appear to have improved. These results should be interpreted cautiously, as relative weight is sensitive to seasonal changes in fish weight (Blackwell et al. 2000), but there is some evidence supporting this trend. We observed more Lake Trout that were large (greater than 600 mm) in 2025 (Figure 10), and it appears that there was a sustained increase in stocking of large (~225 mm) Rainbow Trout *Oncorhynchus mykiss* after 2013 (though the total amount over 10 year periods was similar; Figure 11). It is unclear how this would have translated to increased body condition in Brown Trout, which are generally not piscivorous in Grand Lake and are vulnerable to large Lake Trout. It may be that with a larger portion of the Lake Trout population being piscivorous, there may have been reduced competition for the preferred prey of Brown Trout (e.g., invertebrates). Improving body condition may be associated with increased consumption rates and concomitant reductions or increased predation pressure on their prey, including Mysis. We will evaluate this possibility in conjunction with our pending estimates of fish population size, growth rates, and trophic relationships (via stable isotope and gut content analysis).

We will use the pending results from Phase I to further evaluate the Grand Lake food web and inform Phase II. The current densities, growth rates, and life cycle characteristics of the Grand Lake Mysis population, for example, will directly inform our proposed mesocosm experiments. We will determine the seasonal densities of Mysis to serve as the control for the experiments and then establish reduced Mysis densities in the treatments. Further, we will have information on the trophic links in the Grand Lake food web and the role of Mysis as consumers and prey. For instance, the amount of zooplankton consumed by Mysis will inform how much Mysis would need to be reduced to allow the zooplankton to rebound. Finally, we will link these findings to the long term-data set on Grand Lake to evaluate how nutrients, temperature, and pumping may be influencing the lake's food web and life history characteristics, especially for Mysis and plankton.

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FIGURES

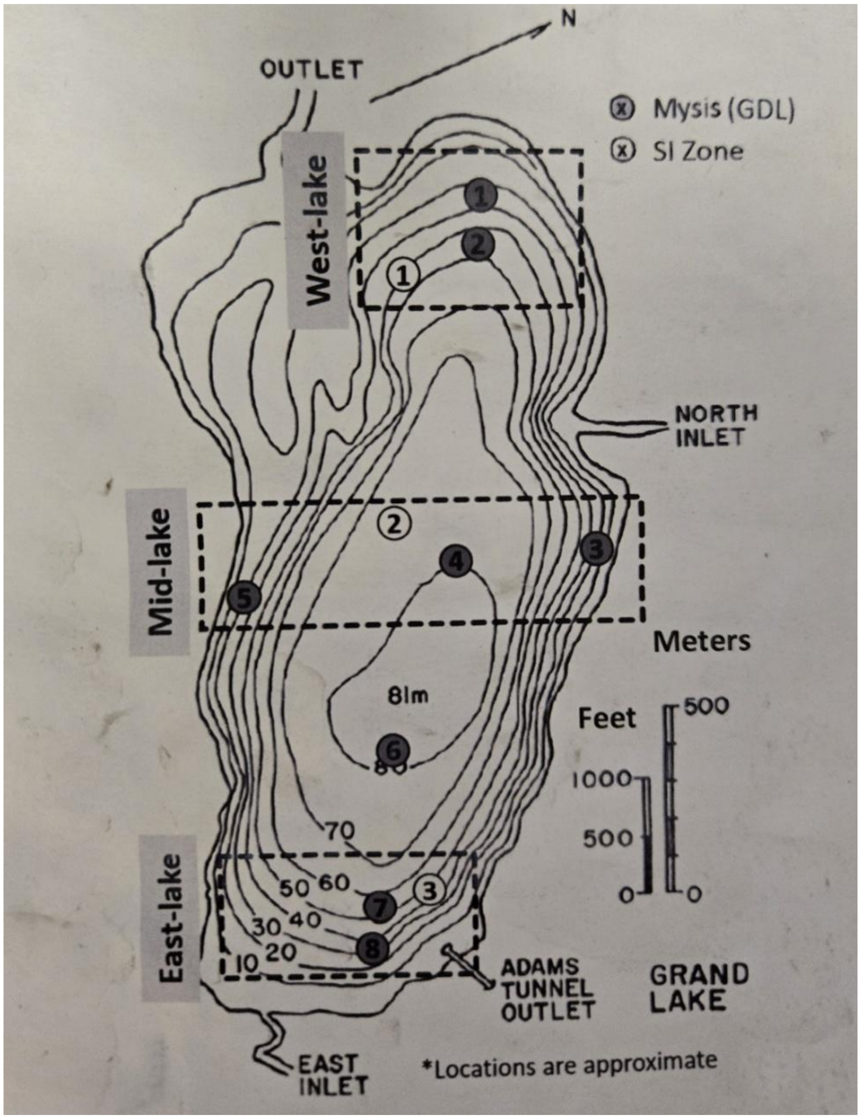


Figure 1. Adapted from Johnson and Pate (2014). Map of Grand Lake sample stations and zones. Dark grey circles indicate where pelagic Mysis samples (1-8) were collected. White circles with the dashed box around them indicate the sample zones (1-3 or West, Mid, and East, respectively) where benthic tows and isotope samples were collected.

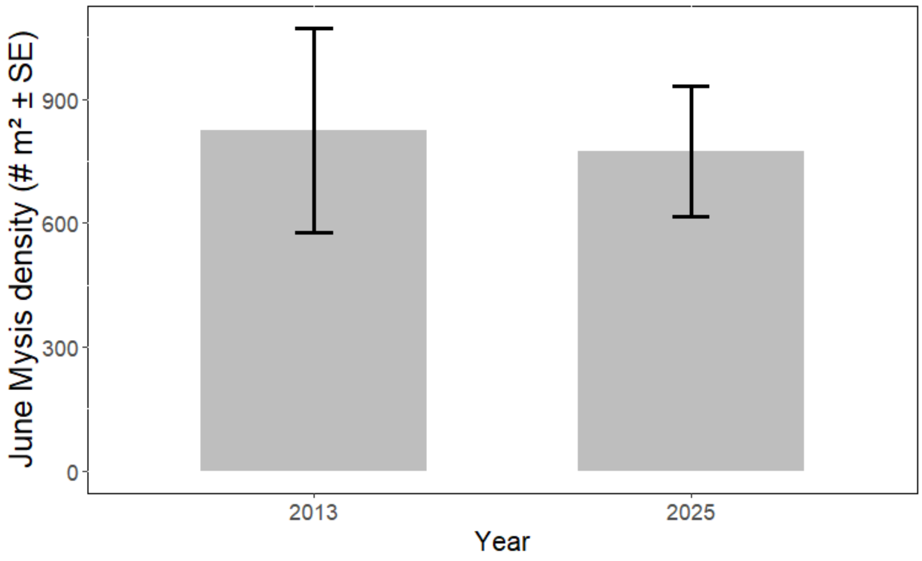


Figure 2. Mean pelagic Mysis densities (#/m^2, ±standard error) in Grand Lake, CO from June 2013 and 2025.

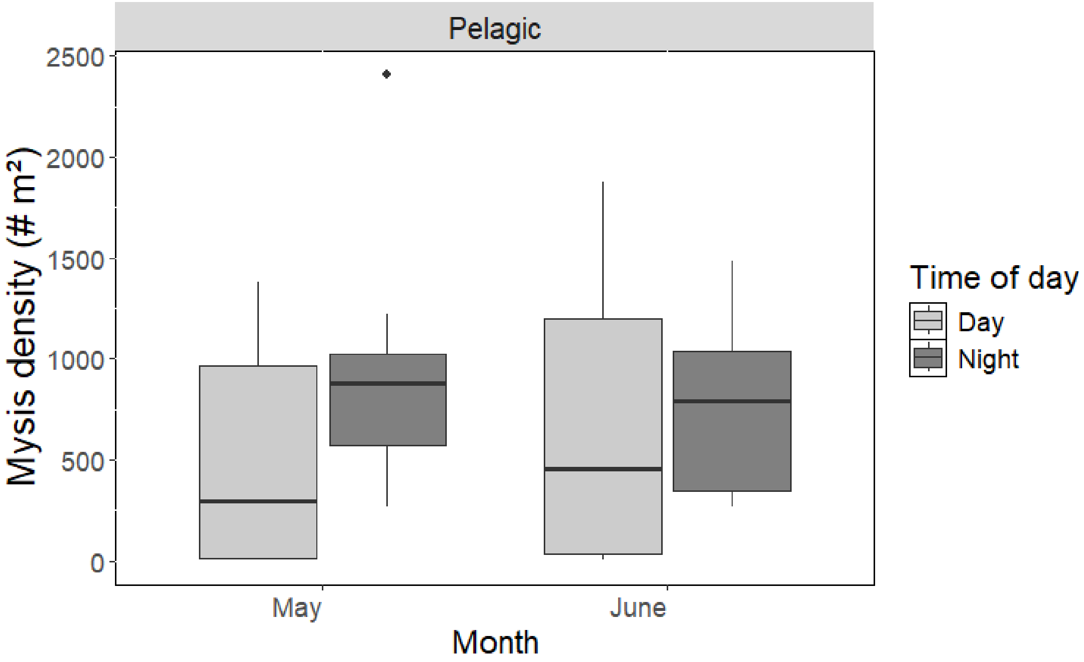


Figure 3. Distribution of pelagic Mysis densities (#/m^2) during the day and night in Grand Lake, CO from May and June 2025.

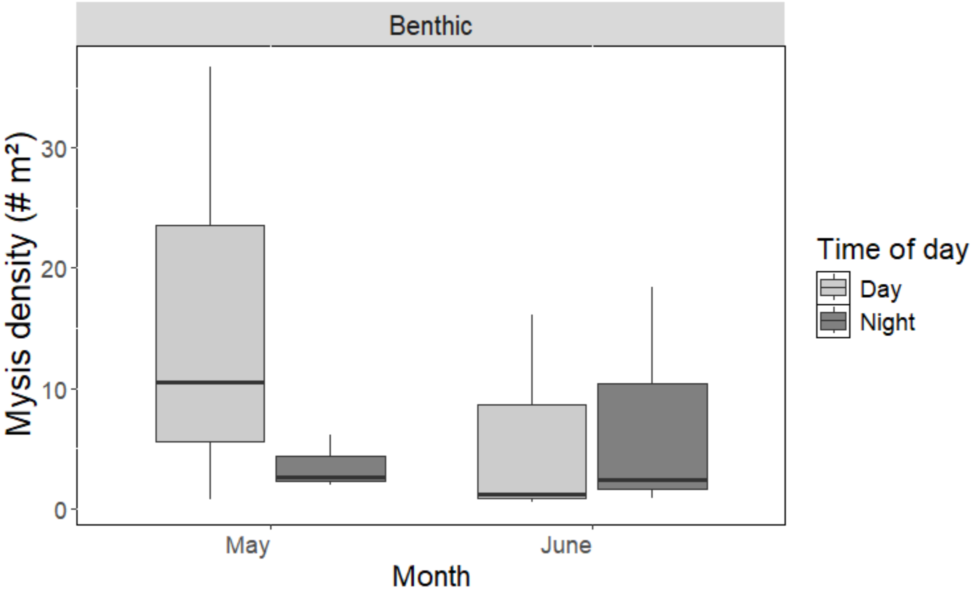


Figure 4. Distribution of benthic Mysis densities (#/m^2) during the day and night in Grand Lake, CO from May and June 2025.

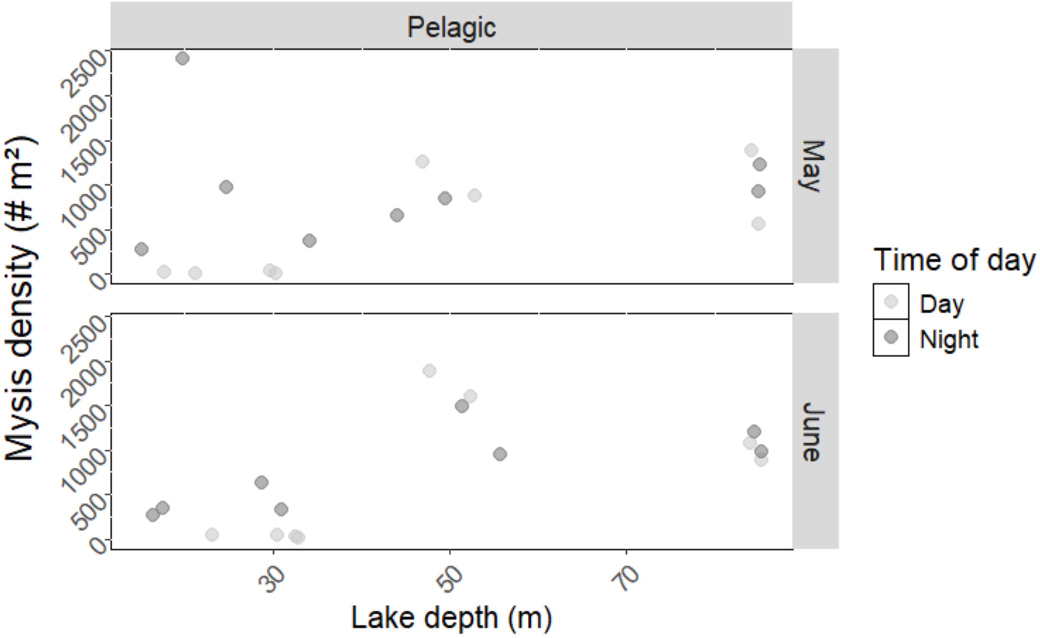


Figure 5. Pelagic Mysis densities (#/m^2) across lake depths and during the day and night in Grand Lake, CO from May and June in 2025.

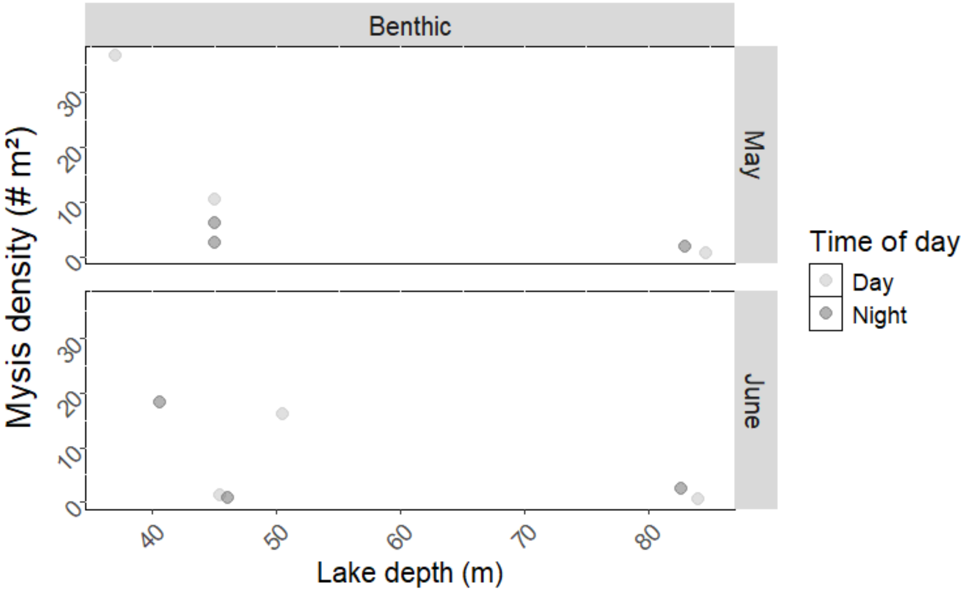


Figure 6. Benthic Mysis densities (#/m^2) across lake depths and during the day and night in Grand Lake, CO from May and June in 2025.

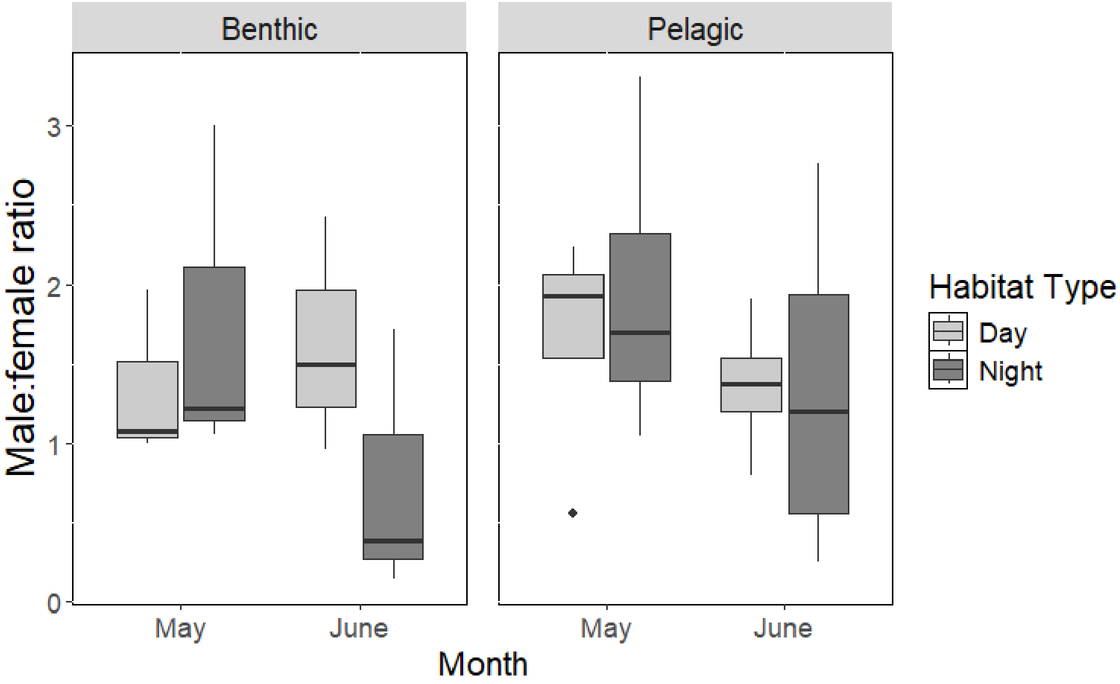


Figure 7. Distribution of Mysis male to female sex ratios from benthic and pelagic habitats during the day and night in Grand Lake, CO. Results shown for May and June in 2025.

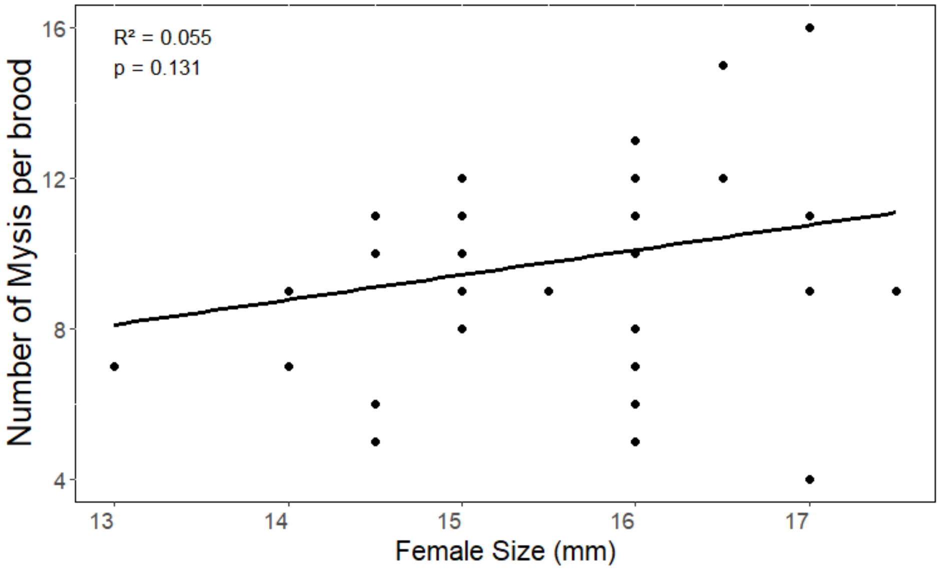


Figure 8. The relationship between Mysis female size (mm) and number of embryos/juveniles in their brood in Grand Lake, CO. Results shown are from May and June in 2025.

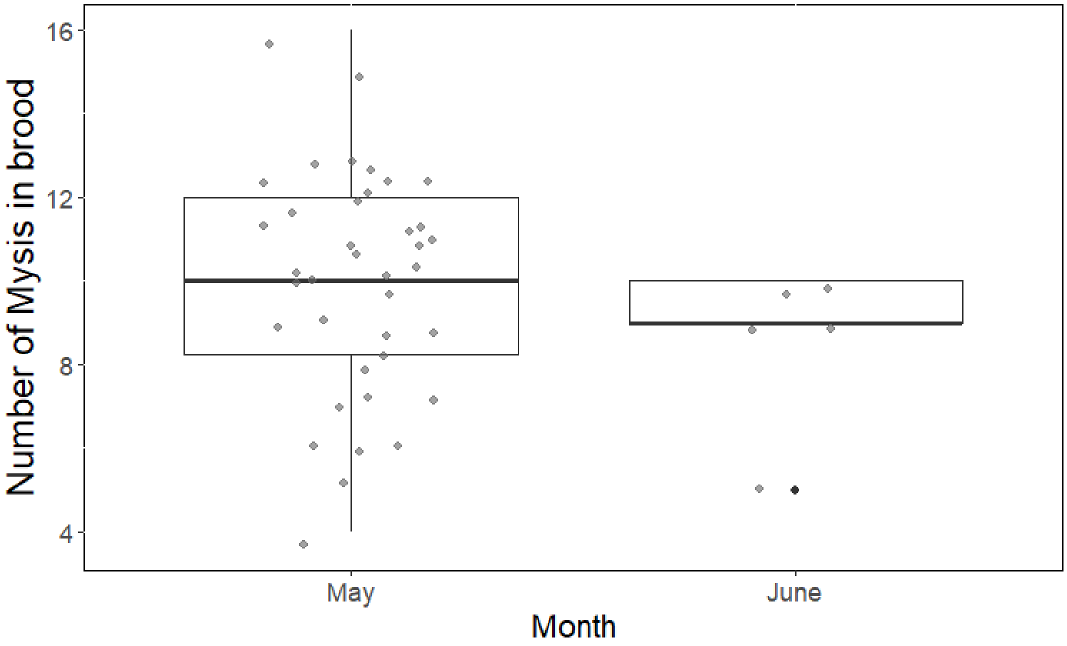


Figure 9. The distribution of Mysis brood counts in Grand Lake, CO from May and June in 2025.

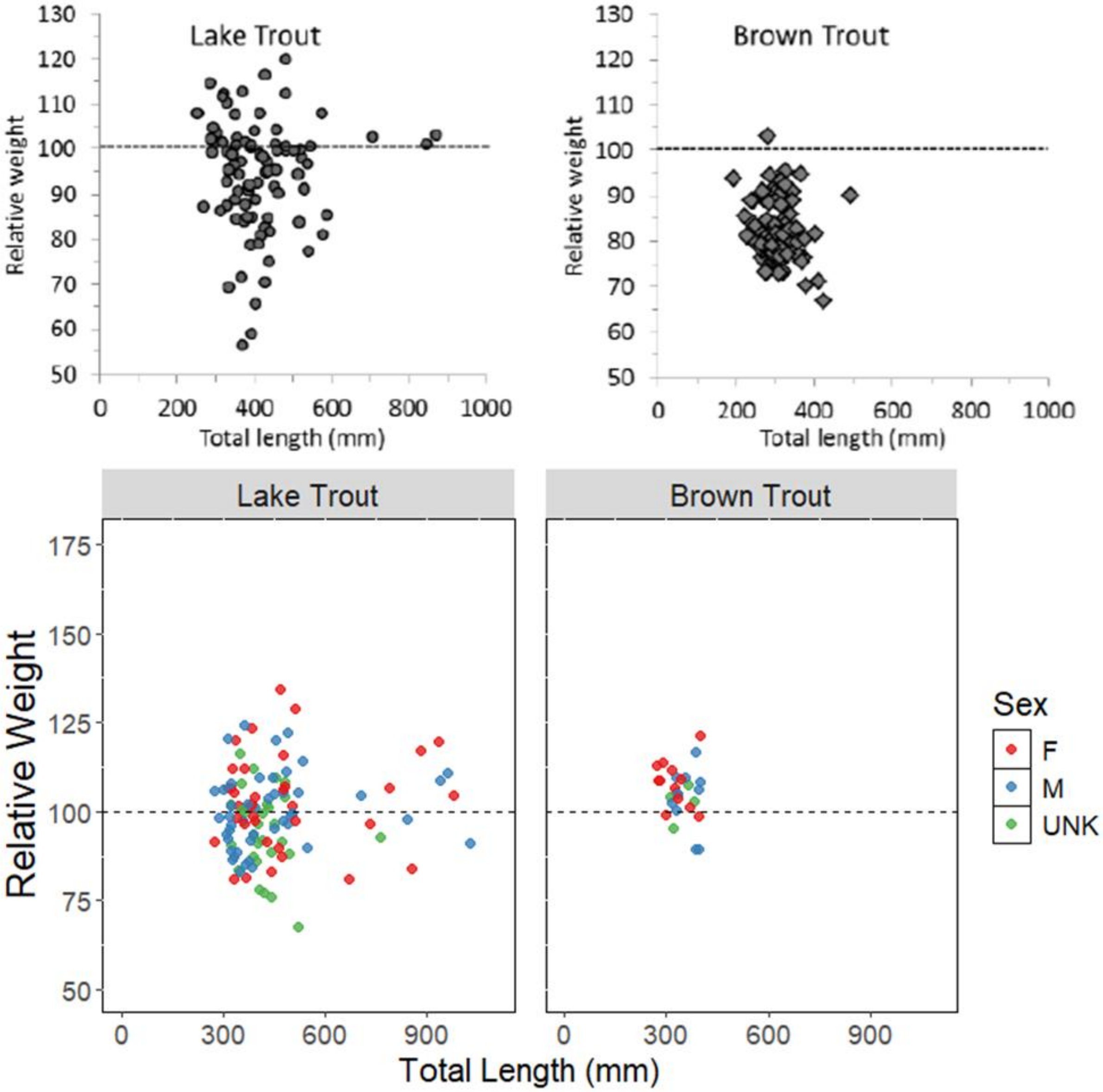
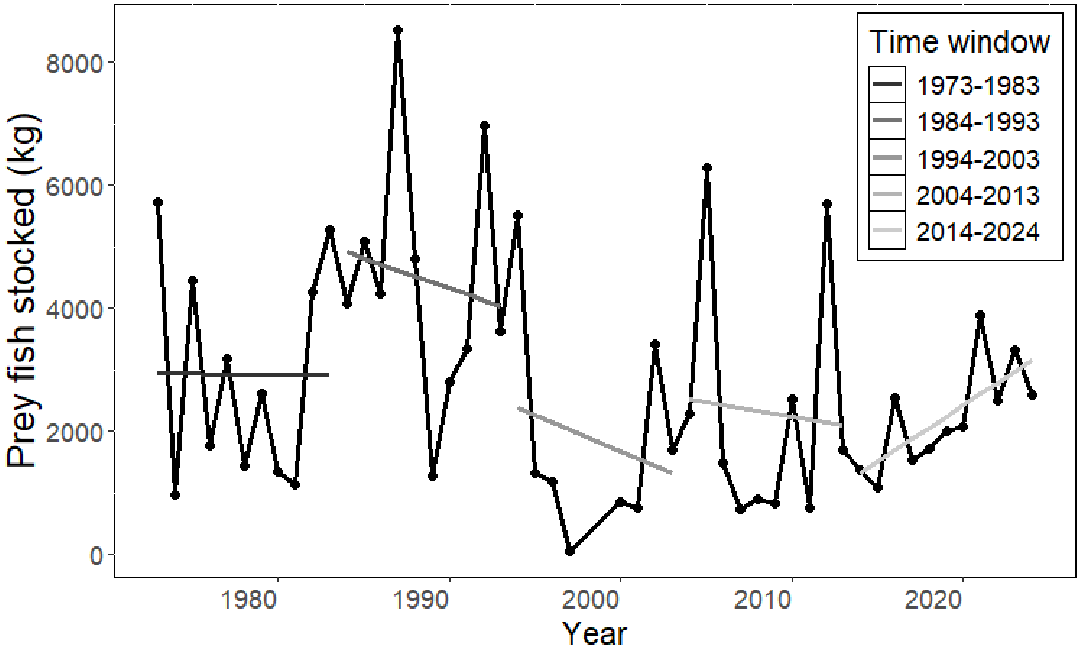


Figure 10. The relationship between total length and relative weight for Lake Trout and Brown Trout in Grand Lake, CO from 2013 (top) and 2025 (bottom). Data for 2013 are from Jonhson and Pate (2014). Individuals from 2025 are colored by sex.



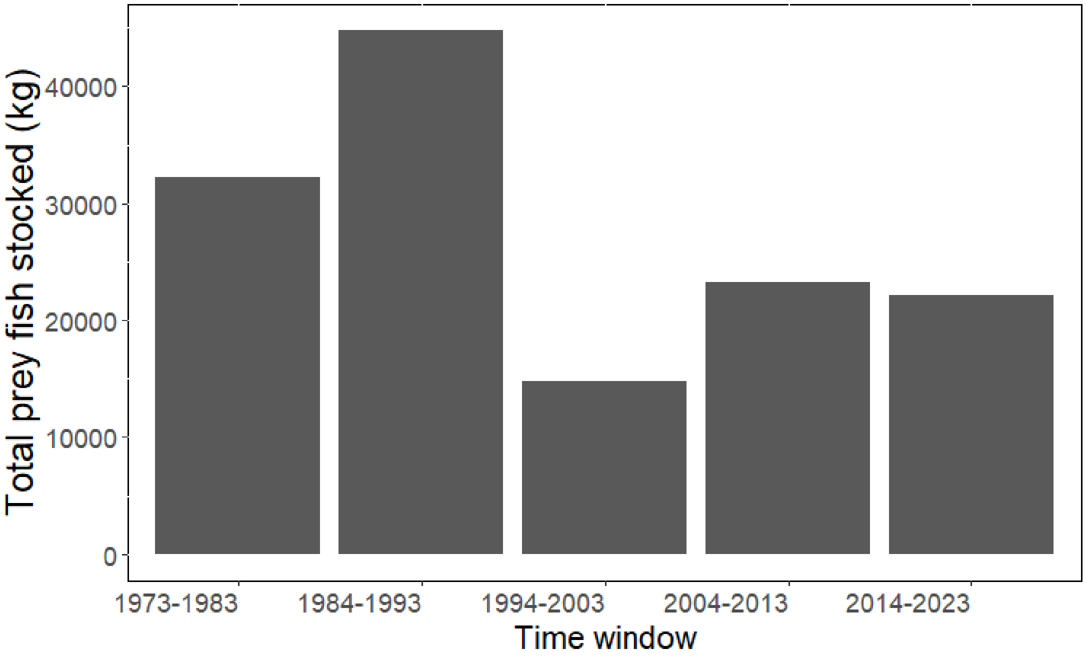


Figure 11. The stocking record of catchable Rainbow Trout (kg) into Grand Lake, CO by year (top) and by 10-year time windows (bottom). The trend in prey fish stocked over time is also shown in 10-year time windows (top), with increments varying by shading.

RESEARCH PRIORITY: **Summer Profundal Index Netting for monitoring Lake Trout:** Results from 2025 sampling on Grand Lake.

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). Five water bodies have been sampled using SPIN: Blue Mesa Reservoir (2011, 2014, 2016, 2018, 2020-2022, and 2024), Grand Lake (2013, 2016, 2025), Lake Granby (2014), Ruedi Reservoir (2023), and Taylor Park Reservoir (2013). Results from the 2025 survey on Grand Lake 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 their density 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 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. 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 two days from August 12-13, 2025 wherein 36 nets were set, capturing a total of 117 Lake Trout ranging in size from 276 mm to 1,024 mm total length (TL; mean = 451 mm ± 160 mm SD). Of the Lake Trout encountered, 65% ranged between 275 and 450 mm TL. Lake Trout were most prevalent in 10-20 m depths, followed by 20-30 m depths. The depth distribution, size structure, and extent of the catch in 2025 produced a total Lake Trout abundance estimate of 2,815 fish ≥276 mm TL (lower 68% confidence limit = 2,288; upper limit = 3,417). The 2025 SPIN estimate was similar to estimates from 2013 and 2016, demonstrating a relatively stable Lake Trout population in Grand Lake (Table 1).

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 fork length [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 correcting the catch for size-selectivity. Asterisks indicate the presence of Mysis.

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
	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
2021											
	Blue Mesa	90	121	465	126	1.23	5.97	1,637	9,775	7,213	12,627
2022											
	Blue Mesa	79	151	364	106	1.45	7.06	1,768	12,477	9,451	15,864
2023											
	Ruedi*	30	106	378	104	6.36	30.90	325	10,050	8,443	11,913
2024											
	Blue Mesa	79	229	447	112	1.75	8.49	2,776	23,573	18,282	29,528
2025											
	Grand Lake*	36	117	451	160	3.00	14.59	193	2,815	2,288	3,417

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RESEARCH PRIORITY: **Evaluating reservoir reoperation:** Blue Mesa Lake Trout population expansion.

OBJECTIVES

Assess the interactive role of drought and dam reoperation and associated water level fluctuations in regulating the population productivity of Lake Trout in Blue Mesa Reservoir. Develop a population model that can be used to inform the ongoing angler harvest incentive program. Prepare and submit a manuscript with findings to a peer-reviewed journal for publication.

PUBLICATION

Hansen, A. G., J. M. Lepak, W. M. Pate, D. Brauch, and **B. W. Avila.** Just water over the dam? Reservoir fishery disruption following drought-mediated reoperation for environmental flows. Ecosphere 16:e70412.

BACKGROUND

Experimental reoperation of Blue Mesa Dam began in 1992 to improve downstream flow conditions for endangered fishes endemic to the Colorado River and its tributaries (Tyus 1992). Traditional operations emphasized stable releases year-round for hydropower generation and elevated releases later in the year to draw the reservoir down over fall and winter to reduce upstream ice damage, capture spring snowmelt, and control flooding. The goal of reoperation was to generate an annual peak flow pulse in spring and more appropriate late-season base flows (while maintaining other critical functions and water agreements; USBOR 2012), both of which are important functional elements of regional snowmelt-driven hydrographs (Van Steeter and Pitlick 1998; Johnson et al. 2004). Between 1992 and 2003, water release patterns were modified to achieve elevated spring flows annually (i.e., environmental flows), and were coupled with independent research to assess reservoir responses. Empirical data and modeling demonstrated that water operators had considerable latitude for modifying releases without affecting the physiochemical properties and productivity of the reservoir, key factors underlying food web interactions (Johnson and Koski 2005). Following this period, contingencies were added for drought, wherein environmental-flow targets and base flow releases were scaled based on inflows during relatively dry versus wet years. Environmental flow operations were formalized in 2012 through completion of the US National Environmental Policy Act Review Process (USBOR 2012). In order to achieve drought-mediated environmental flow targets, the seasonal pattern of water releases were modified. After reoperation, relative releases were generally lower during fall and winter (Lake Trout spawning and egg incubation period) and higher during spring versus traditional operations in both relatively wet and dry years (Figure 1B,C; Johnson and Koski 2005; USBOR 2012).

Coinciding with the reoperation of Blue Mesa Dam, the population of Lake Trout within the reservoir expanded, leading to unsustainable predator-prey interactions with other salmonid sport fish and a series of ongoing management interventions to mitigate negative effects. An association between reoperation and Lake Trout expansion has long been part of the Blue Mesa Reservoir fishery narrative, but evidence for this link has not been examined explicitly. Therefore, long-term fisheries-dependent (e.g., creel surveys) and fisheries-independent (e.g., SPIN surveys) data were integrated into a population modeling framework to test whether reoperation was a plausible driver of Lake Trout expansion. The model estimated the intrinsic population productivity of Lake Trout under different water management regimes and can be used to inform ongoing angler harvest incentive tournaments.

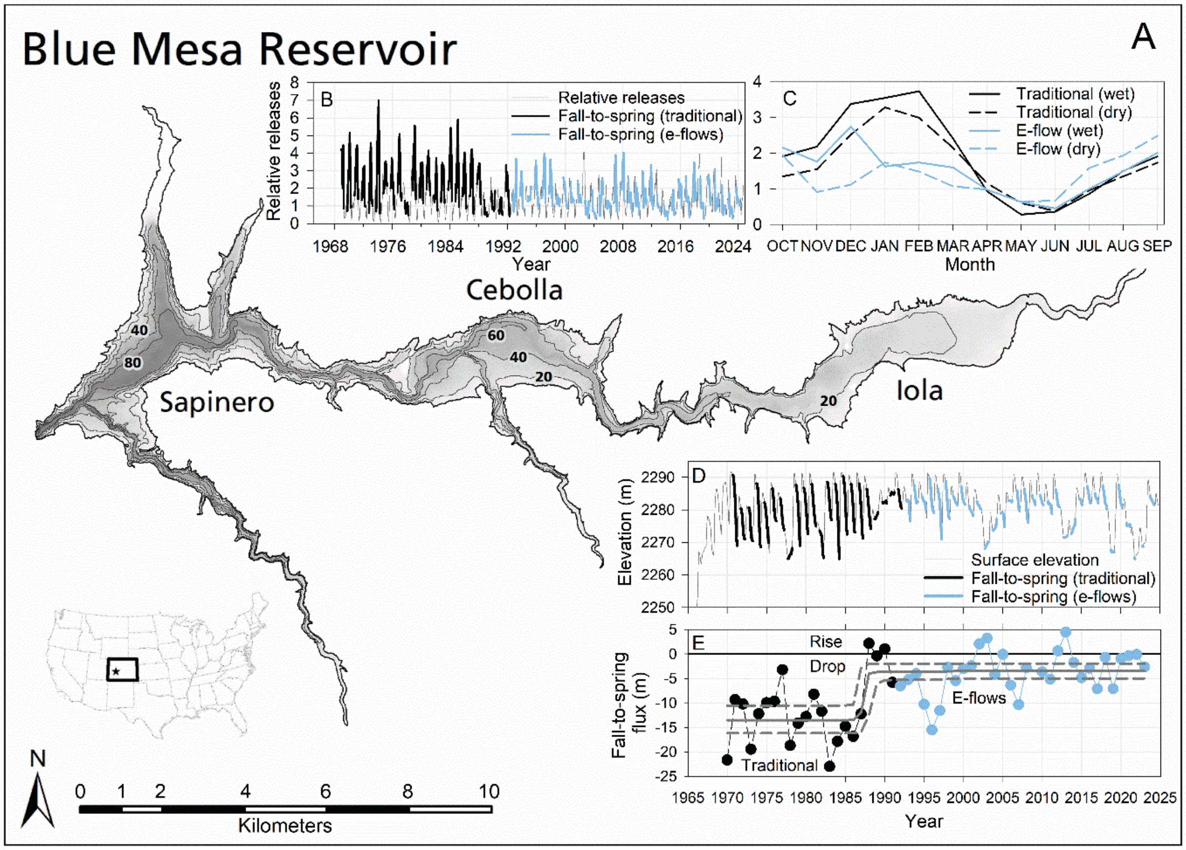

Figure 1. Blue Mesa Reservoir. (A) Bathymetric map (20 m contours) with main basins labeled. (B) Time series of total relative dam releases (monthly means in CMS [$m^3 \cdot s^{-1}$]) with the fall-to-spring period (October—April) highlighted while under traditional dam operations and those for environmental flows (e-flows). Releases were scaled by dividing by corresponding reservoir inflows (CMS). (C) Relative releases by month averaged across years under each operational regime and parsed by relatively wet versus dry years. Wet years were defined as those in which the reservoir achieved ≥95% of its live storage capacity while dry years were <95%. (D) Time series of reservoir surface elevations (monthly means) with the period contributing to the computation of fall-to-spring flux highlighted for each operational regime. (E) Time series for the magnitude of fall-to-spring flux for each operational regime (points) and the fitted change-point regression model with 95% credible intervals identifying distinct regimes (solid and dashed gray lines, respectively).

PUBLICATION ABSTRACT

Environmental flow (e-flow) management is a growing driver of dam reoperation in which impounded water is allocated to rivers for ecosystem benefits. However, the effects of reoperation on reservoir ecosystems remain largely unstudied, despite their global importance in providing critical social-ecological services (e.g., fisheries, food and water security). This deficiency has limited our ability to conduct inclusive assessments of the multi-use tradeoffs associated with reoperation. Here, we compiled fisheries survey data spanning five decades to evaluate potential responses to the e-flow-driven reoperation of a large montane reservoir in the arid southwestern United States. Following reoperation, seasonal water release patterns were modified, and late-season reservoir drawdowns diminished by 74% (13.6 m to 3.5 m on average). Reoperation coincided with the population expansion of an introduced apex predator, destabilization of a recreational fishery, and adaptation by fisheries managers to mitigate. The degree and timing of late-season water level stabilization was sufficient to facilitate predator reproduction. An exponential growth modeling framework, grounded in principles of invasion ecology, demonstrated that a two-stage (versus one-stage) population productivity process was required to explain patterns in survey data and to generate biologically relevant parameter estimates. This outcome indicated that predator expansion was not strictly inherent. Processes (e.g., system productivity) other than changes to seasonal water level fluctuations could not explain the expansion. Collectively, results lend evidence that reoperation was a plausible contributing factor to predator expansion, which disrupted reservoir services. Importantly however, e-flow operations were mediated by periodic drought. Late-season drawdowns were reduced during relatively wet years, partially reflecting modifications to seasonal releases to help facilitate e-flows, but also during drier years to mitigate storage loss. Thus, these processes were not independent and operated in tandem. More comprehensive understanding of the reciprocal effects of drought-mediated reoperation may improve our ability to manage impoundments to better meet multiple conservation and societal objectives while adapting to change across a broad spectrum of drivers and social-ecological contexts. Hydroclimate may ultimately be an overriding process regulating dam operations, reservoir water levels, and delivery of effective e-flows given expected increases in drought frequency and severity in arid and semi-arid regions.

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<u>RESEARCH PRIORITY</u>: **Understanding Gizzard Shad *Dorosoma cepadianum* in Colorado.** Technical Publication: Gizzard Shad in Colorado lakes, reservoirs and ponds: background, generalizations, system-specific examples, control, and alternatives.

OBJECTIVES

Use existing data and information coupled with research efforts to better understand potential interactions between Gizzard Shad and important native and sport fish species in lakes and reservoirs, and to describe the distribution and relative success of Gizzard Shad across the Colorado landscape.

TECHNICAL PUBLICATION

Lepak, J. M., A. G. Hansen, A. J. Treble, and E. Stewart Krone. 2025. Gizzard Shad (*Dorosoma cepedianum*) in Colorado lakes, reservoirs and ponds: background, generalizations, system-specific examples, control, and alternatives. Colorado Parks and Wildlife Technical Publication No. 67.

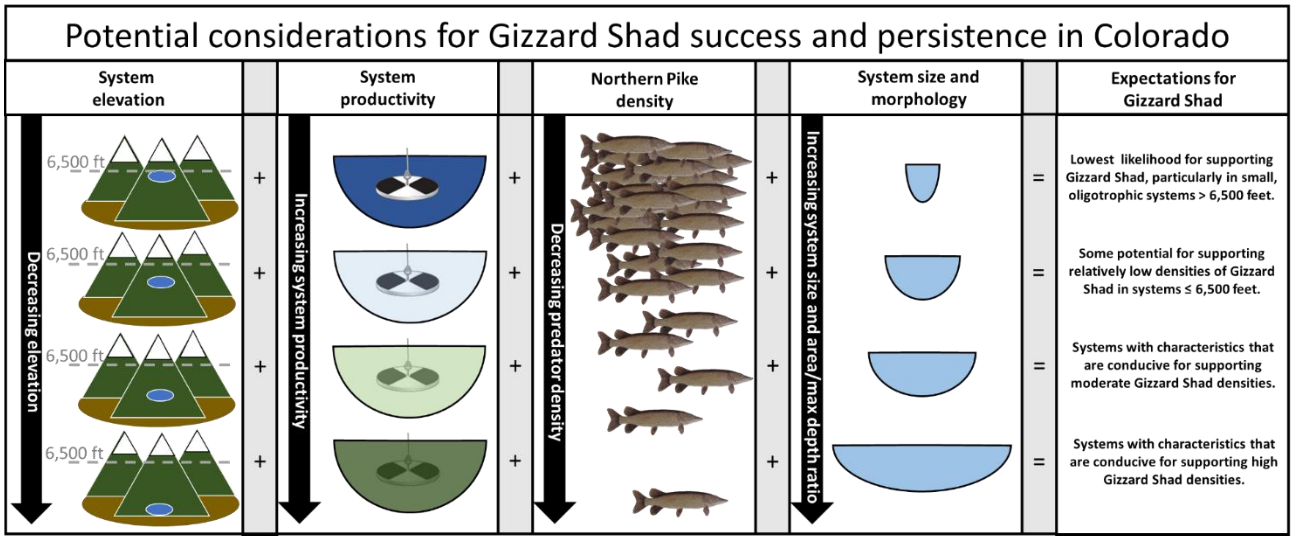
BACKGROUND

Gizzard Shad are native to the western Great Plains and were spread throughout Colorado including areas on the Western Slope, in most cases to provide additional foraging opportunities for sport fish. Gizzard Shad can be highly-prolific (Stein et al. 1995), and because of this, their numbers post-spawning (including young-of-year individuals) can exceed those of most other fish species in the systems they occupy. At the same time, Gizzard Shad often experience significant die-offs, especially following harsh winters (e.g., extended low temperatures), and this results in population fluctuations largely dependent on stochastic events (Miller 1960; Fetzer et al. 2011). Thus, Gizzard Shad provide a potentially significant, yet variable, food resource for many predators. This food resource is especially important when Gizzard Shad are relatively young, small, abundant, and vulnerable to predation by most predators.

Data are available in Colorado to better understand the role of Gizzard Shad, and their potential to interact with various sport fish species in lake and reservoir food webs. A total of more than 300,000 Gizzard Shad have been sampled in Colorado and reported within ADAMAS from sampling events starting in 1964 through 2023. Of these 300,000 Gizzard Shad, 176,000 were counted (~58%) and 128,000 were reported as measured (~42%) across all waterbodies. During this same time period, Gizzard Shad (79,061 individuals) were sampled and measured from 240 Colorado lake/pond/reservoir systems (excluding reports from lotic systems). Using these data, we hope to inform fisheries managers about important Gizzard Shad characteristics and potential interactions with other fish species throughout Colorado. We focus primarily on Gizzard Shad distribution and characteristics influencing their interactions with predators (e.g., persistence, growth, timing of spawning/hatching) in Colorado lakes and reservoirs.

TECHNICAL PUBLICATION GRAPHICAL ABSTRACT

Generalized expectations for Gizzard Shad populations in Colorado systems with gradients of different characteristics:



TECHNICAL PUBLICATION EXECUTIVE SUMMARY

- Gizzard Shad are a prolific forage fish that has spread throughout Colorado, though there is some debate about their status.

- Gizzard Shad can provide forage for predators, but also represent a competitor with some larval and juvenile fishes for zooplankton resources.

- Hundreds of thousands of Gizzard Shad have been sampled in Colorado, and more than 75 attempts have been made to establish populations in systems with few or no shad.

- There is evidence of late or prolonged spawning of Gizzard Shad in some systems with spawning likely beginning as early as March and continuing through September, and many systems have not been sampled late enough to determine the prevalence of late or prolonged spawning.

- Catches of Gizzard Shad appeared to be correlated with multiple variables, though caution should be used interpreting these data as sampling frequency and intensity can also be correlated with some of the variables considered.

- Catches of Gizzard Shad were higher in systems that were larger in surface area compared to smaller systems.

- Gizzard Shad catches were higher in systems that were lower in elevation (likely warmer) compared to systems at higher elevations, and Gizzard Shad were not observed in systems with elevations exceeding 6,500 feet.

- Systems that were more productive based on chlorophyll a, Secchi depth, and Trophic Status Index had higher catches of Gizzard Shad, though there is likely some threshold where productivity may exceed what is suitable for Gizzard Shad.

- Systems with higher surface area to maximum depth ratios had higher catches of Gizzard Shad relative to systems with lower area/maximum depth ratios.

- Gizzard Shad catches can be variable and gear-specific, and consideration must be given to how and when Gizzard Shad are sampled to develop valuable catch-per-unit-effort information.

- Success of Gizzard Shad transplants likely relies on multiple factors described above (i.e., system size and morphology, elevation, productivity) and potentially other factors like the presence of invasive species (e.g., Eurasian watermilfoil) or predators (e.g., Walleye *Sander vitreus*, Largemouth Bass *Micropterus salmoides*).

- Some systems with Gizzard Shad appear to support robust predator populations and stocking programs (contributing to the growth and survival sport fish) even though Gizzard Shad catch rates are low or variable, suggesting other gears or sampling designs might be beneficial to characterize forage, or that Gizzard Shad numbers may appear low because they are being consumed by the predators they support, but are still present and productive.

- Based on data collected in 2021 from Chatfield and Cherry Creek reservoirs, Cherry Creek Reservoir offered more favorable conditions for Walleye with higher densities of zooplankton forage for young-of-year Walleye, warmer water temperatures beginning in May, higher turbidity, later emergence of Gizzard Shad in size classes available as forage for young-of-year Walleye, and ultimately more rapid growth of young-of-year Walleye.

- Several techniques have been used with varying degrees of success to control/manage Gizzard Shad populations including dewatering, rotenone treatments, stocking Gizzard Shad predators, gillnetting, and electrofishing, however, many researchers suggest that resources dedicated to Gizzard Shad removal should be focused instead on sport fish management efforts.

- Multiple species were considered as potential alternatives to Gizzard Shad as forage for sport fish considering their native status, previous introductions in Colorado, and potential for success/persistence, overpopulating systems, providing accessible/available prey for sport fish.

- Many species considered as alternatives to Gizzard Shad had limitations related to temperature (potentially too cold/warm for success/persistence across the large gradient of Colorado elevation) or other factors that may have negative impacts on sport fish populations.

- Golden Shiner *Notemigonus crysoleucas* were selected as one of the most versatile and innocuous alternative sport fish forage species to Gizzard Shad in Colorado, being observed in over 100 lentic systems at elevations from 3,520 to 9,225 feet, and achieving maximum sizes that are within the gape limitations of predators like Walleye.

- Monitoring efforts targeting prey fish species specifically have the potential to further inform sport fish management in Colorado and there is value in rigorous and long-term data collection from forage fish to inform the status of predator populations that rely on these resources.

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RESEARCH PRIORITY: **Evaluating tiger muskellunge (Northern pike *Esox lucius* × Muskellunge *E. masquinongy*) as a multi-purpose management tool:** Protecting native fish species from multiple conservation threats.

OBJECTIVES

To evaluate stocking tiger muskellunge as a means to disadvantage introduced species (Northern Pike, Smallmouth Bass *M. dolomieu*, and White Sucker), while simultaneously diminishing motivation to illicitly transplant non-native predators that negatively impact native fish species and whole ecosystems. Overall objectives include:

- Improving conditions for native fish by disadvantaging non-native predators (Northern Pike and Smallmouth Bass) that have been illegally introduced, and undesirable species that are spreading in Colorado like White Suckers.

- A controllable method for disadvantaging nuisance species that is compatible (sterile hybrid) with native fish conservation goals, and discouraging further spread/introduction of non-native predators.

One of the biggest threats to the protection and conservation of native fishes in Colorado is the spread of invasive species. The information gained from this project will provide an indication of the efficacy of tiger muskellunge stocking as a management tool in Shadow Mountain and Elkhead reservoirs to combat factors threatening native fishes in Colorado.

BACKGROUND

Threats to native fish species in Colorado are ubiquitous and come in many forms. For example, illicit stocking of predators (e.g., Northern Pike and Smallmouth Bass) in Colorado has been occurring for decades, and remains a salient issue. These invasive species can consume native fishes (e.g., Cutthroat Trout *O. clarkii*) directly, and also compete for prey and other resources. In addition to non-native predator introductions, native fish species can be exposed to organisms that non-native fishes support. For example, gill lice *Salmincola californiensis* are an external parasite of Pacific salmonines, including Cutthroat Trout, Mountain Whitefish *Prosopium williamsoni*, and Rainbow Trout, among other species (Hoffman 1999; Barndt and Stone 2003).

Curtailing illicit species introductions, and addressing their negative consequences when they do occur, is imperative for protecting native fishes. Similarly, slowing the spread, and addressing the impacts of parasites on native fishes is also important for sustaining their populations. To address these issues and obtain useful information for managers, Colorado Parks and Wildlife (CPW) has proposed the use of tiger muskellunge (sterile Northern Pike and Muskellunge hybrids) stocking as a means to disadvantage introduced species (Northern Pike, Smallmouth Bass, and White Sucker) and provide a species compatible (sterile hybrid) with native fish conservation goals to discourage the illegal spread/introduction of non-native species. This approach also has potential to slow the spread of gill lice to native fish populations in some situations, complementing CPW's other species conservation work on gill lice control efforts. This approach supports native fish protection efforts in the Yampa River and Colorado River basins, and could help diminish motivation to illicitly transplant non-native predators that negatively impact native fish species.

The need for innocuous or controllable fish species that are compatible with native fish conservation goals is evident in Colorado. For example, there was (and still is) high demand for tiger muskellunge to stock in Colorado waters (nearly 100,000 requested and provided in the early 1990's). This need is highlighted further by efforts currently underway in Colorado to develop sterile fish species (e.g., triploid Walleye) that will have relatively predictable and ephemeral impacts for stocking in areas where they may interact with native fish species.

Tiger muskellunge reach relatively large sizes, and have some of the highest potential to disadvantage undesirable species like White Suckers, and introduced predators like Northern Pike and Smallmouth Bass, when stocking of naïve salmonids, a preferred esocid prey item (Lepak et al. 2012; Lepak et al. 2014), is minimized. In Colorado, however, catchable salmonids are often stocked in systems where tiger muskellunge are present, and detailed investigations where salmonids are not stocked in conjunction with tiger muskellunge are lacking. Thus, a direct benefit of this project would be a formal evaluation of tiger muskellunge stocking under conditions (minimal stocking of potential forage) to further optimize their application and provide benefits to native fish species. This is in contrast to a previous study where tiger muskellunge efficacy was evaluated in reservoirs where stocking forage (salmonids) was occurring, and subsequently consumed by tiger muskellunge (Lepak et al. 2014).

PROJECT PROGRESS

Shadow Mountain Reservoir

- As of July 2025, over 23,000 tiger muskellunge have been stocked in Shadow Mountain Reservoir. Of these tiger muskellunge, over 15,000 were marked with PIT tags, 42% (5,400) of the 13,000 individuals stocked in 2023, and all those stocked in 2024 (3,700) and 2025 (6,500).

- The fish were stocked by boat and distributed in protected areas with structure around the islands of Shadow Mountain Reservoir, primarily on the southern end.

- Routine gillnetting (20 experimental gill nets for 6-hour daylight sets) in 2025 took place in early June, and

PIT tagging tiger muskellunge at the Wray Hatchery.

produced 46 tiger muskellunge, presumably from the 2023 plant based on their size and PIT tag numbers.

- At stocking in 2023, mean lengths and weights of tiger muskellunge stocked were 203 mm and 44 grams.

- The 46 tiger muskellunge captured in 2025 had a mean length of ~464 mm and a mean weight of ~682 grams indicating significant growth since stocking.

Tiger muskellunge captured while electrofishing Shadow Mountain Reservoir.

- Of the 46 tiger muskellunge captured, 26 were released and 20 were retained for chemical testing to determine diet.

- Of the 26 individuals released, nine (35%) were tagged. In 2023, approximately 42% of the tiger muskellunge stocked were tagged, which generally aligns with these data (similar ratios of tagged to untagged fish).

- Of the nine tagged fish, four were from Nebraska, and five were from Pennsylvania. In this 2023 batch of stocked tiger muskellunge more fish from Pennsylvania were marked (3,189 versus 2,304) because survival after PIT tagging was significantly higher for fish originating from Pennsylvania.

- Small White Suckers from this survey (n = 11) along with small Brown Trout (n = 3) and Rainbow Trout (n = 2) mortalities were collected for stable isotope analyses to determine the diet composition of tiger muskellunge.

- Additional prey fish (primarily Iowa Darters *Etheostoma exile*) were collected mid-summer in conjunction with another project for stable isotope analyses.

- Electrofishing took place in July 2025 (we acknowledge Area Biologist G. Dean and crew for making this possible) just four days after tiger muskellunge stocking. During this effort, five Brown Trout large enough to consume tiger muskellunge stocked in 2025 (all PIT tagged) were captured and their stomachs were scanned for PIT tags. No PIT tags were detected that would indicate predation on tiger muskellunge by Brown Trout.

- Catches of larger-sized tiger muskellunge in Lake Granby have been reported to Area Biologist J. Ewert, indicating relatively rapid growth, and some movement to the reservoir below Shadow Mountain Reservoir.

- No tiger muskellunge have been detected on the antenna arrays downstream of Lake Granby in the Colorado River.

Elkhead Reservoir

- Trap nets (5-6) were set in Elkhead Reservoir in mid-April to mark Northern Pike for the annual angler incentivized tournament. Hundreds of individuals were tagged with Floy tags and released to gain information about the Northern Pike population and the efficacy of control measures.

- During the trap net survey (described above), spawning Northern Pike are targeted to increase catch rates, and female Northern Pike are stripped of their eggs prior to release to inhibit reproduction.

- Although mature Northern Pike were found in the survey described above, no tiger muskellunge were observed. Further, no tiger muskellunge have ever been captured during spring trap netting surveys in Elkhead Reservoir since holdover tiger muskellunge stocking began in 2022.

- Boat electrofishing was conducted in Elkhead Reservoir in Mid-June to mark Smallmouth Bass for the annual angler incentivized tournament, and to gain information about the Smallmouth Bass population and the efficacy of control measures.

- No holdover tiger muskellunge were available to stock in 2025 due to the necessary closure of the Wray Hatchery over winter for repairs.

- Small (~200 mm) tiger muskellunge (n = 3,000) were tagged at the Wray hatchery with Floy tags. These fish were stocked in Elkhead Reservoir on 17 July 2025. Tiger muskellunge were stocked in a protected cove with structure and vegetation.

- Northern Pike from the 2024 tournament were processed and tissue samples were taken from these fish with a focus on those that were similar in size to the three tiger muskellunge collected from Elkhead Reservoir during sampling thus far. We will compare stable isotope measurements of Northern Pike and tiger muskellunge tissue to determine the level of potential diet overlap.

- Smallmouth Bass from the 2024 tournament have yet to be processed, and Northern Pike and Smallmouth Bass from the 2025 tournament were collected and are currently being held frozen at the CPW Meeker Office for future processing.

Tiger muskellunge interactions with Northern Pike

Based on data compiled to date, stocking small (150-200 mm) tiger muskellunge can produce desired outcomes (i.e., reductions in catch rates of bullhead and sucker species) under the right circumstances (reducing Rainbow Trout stocking that acts as a buffer between tiger muskellunge and the undesirable target prey species) and in the absence of predators like Northern Pike. However, more information is needed to determine if small and large tiger muskellunge can contribute significantly to management goals (undesirable fish species control) in the presence of dense populations of large predators like Northern Pike. This concept is being evaluated in Elkhead Reservoir, though multiple Northern Pike control measures (i.e., tiger muskellunge stocking, incentivized angling tournament, removing eggs from females captured during spring marking efforts) are being used to suppress their population, confounding data interpretation to some degree. Within this context and to establish baseline conditions of the Northern Pike population, work was initiated in College Lake in collaboration with the Colorado State University (CSU) American Fisheries Society and Drs. Kanno and Myrick in spring 2024. This work has continued with newly hired Dr. Zoe Almeida with CSU.

College Lake represents a controlled, well-studied, closed system where harvest by anglers is not allowed. This lake is an ideal situation to evaluate interactions between stocked TGMs and Northern Pike in more detail. We would like to stock large (holdover) and small (~150-200 mm) tiger muskellunge simultaneously in College Lake in spring 2026. We intend to match the pike population estimate (~1,000) with small tiger muskellunge in addition to a plant of holdover (~100) tiger muskellunge. This would represent relatively high densities of small tiger muskellunge (about 160% to 170%) compared to the 10 fish per acre that has often been used by CPW personnel. We intend to stock large tiger muskellunge at approximately one-tenth the density of the small tiger muskellunge. These fish would all be PIT tagged and Floy tagged to evaluate tag retention and track the fish through time. Finally, we intend to angle intensively after stocking to capture pike specifically and scan their stomachs for PIT tagged tiger muskellunge to quantify tiger muskellunge predation by Northern Pike.

We also have the opportunity to inform the value of stocking fish by boat. We intend to stock half of both size classes of tiger muskellunge by boat along the shoreline into cover, and the other half directly at the boat launch. Over time, we will evaluate survival of individuals to help us understand the potential benefits (or lack-there-of) of raising tiger muskellunge to holdover size and stocking them by boat into cover in predator-dense systems.

Overall project components

- Fish eye lenses may archive changes in diet, growing analogous to tree ring structures (Wallace et al. 2014). However, the technique is relatively new and untested, particularly in freshwater fish. In addition, processing/delaminating fish eye lenses can be challenging, and more work is needed to improve reproducibility of the technique as well as enhance confidence in how to interpret the findings (Chu et al. 2025).

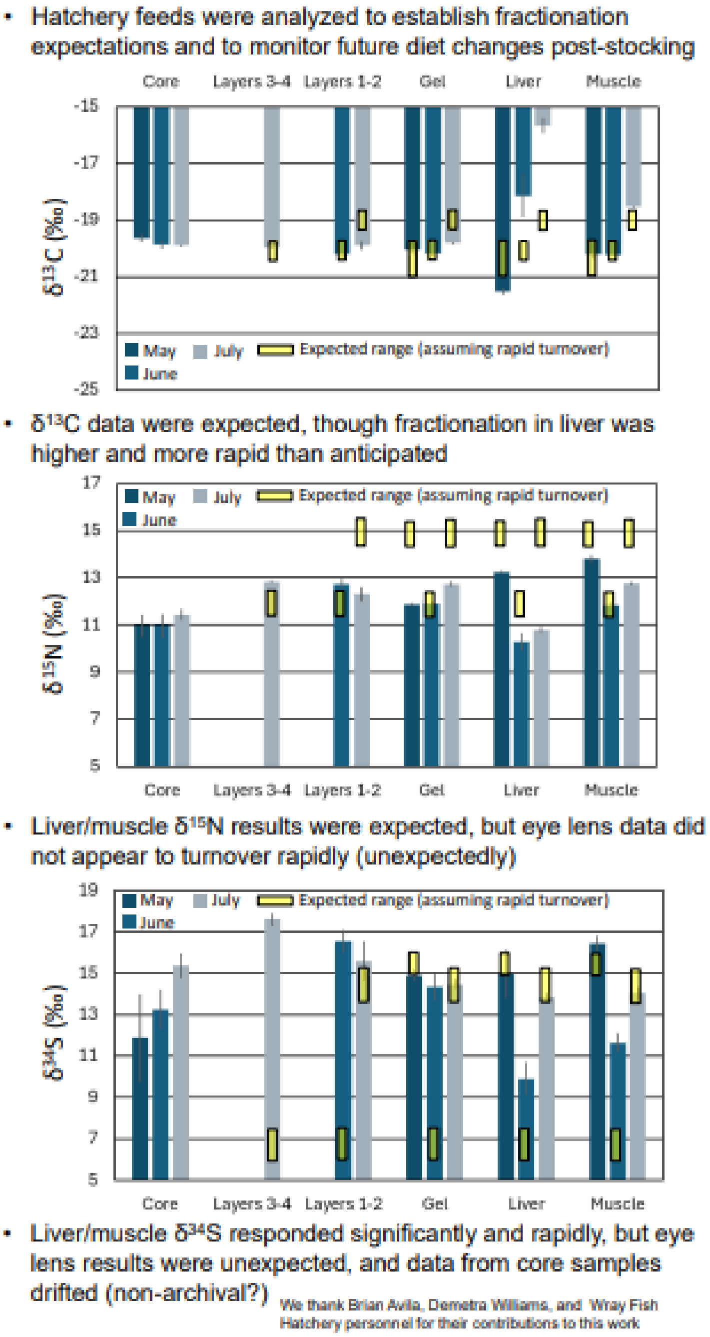
- We analyzed $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of eye lens cores, outer gels, inner layers, liver, and muscle tissues of tiger muskellunge raised at the Wray Hatchery over a 3-month period.

- We presented preliminary results from these analyses as a poster at the American Fisheries Society Western Division Meeting (May, 2025 Westminster, CO).

- Although some results were expected, there were also results disparate from expectation, and more work needs to be done to better understand the archival nature of fish eye lenses (see poster results at right).

- Chu et al. (2025) noted that using measured distances for eye lens analyses reduced subjective error associated with having eye lens processors “count” laminae to determine relationships of isotope measurements to otolith measurements and interpreted ages. We intend to use this technique to refine our observations.

- A Ph.D. student has accepted a position with Dr. Zoe Almeida (CSU) to work on tiger muskellunge and control of non-native species in Colorado. The student will focus on tiger muskellunge data in-hand, responses to tiger muskellunge stocking in College Lake, Elkhead Reservoir, and Shadow Mountain Reservoir, and other potential control methods for non-native species.



- Hatchery feeds were analyzed to establish fractionation expectations and to monitor future diet changes post-stocking

- $\delta^{13}C$ data were expected, though fractionation in liver was higher and more rapid than anticipated

- Liver/muscle $\delta^{15}N$ results were expected, but eye lens data did not appear to turnover rapidly (unexpectedly)

- Liver/muscle $\delta^{34}S$ responded significantly and rapidly, but eye lens results were unexpected, and data from core samples drifted (non-archival?)

We thank Brian Avila, Demetra Williams, and Wray Fish Hatchery personnel for their contributions to this work

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RESEARCH PRIORITY: **Food webs and predator-prey interactions (Part 1):** Predicting Walleye recruitment failure in Horsetooth Reservoir.

OBJECTIVES

To determine the best predictors of Walleye recruitment failure in Horsetooth Reservoir and to prepare and submit a manuscript with our findings.

PUBLICATION

Lepak, J. M., A. G. Hansen, B. M. Johnson, K. Battige, E. T. Cristan, C. J. Farrell, W. M. Pate, **K. B. Rogers, A. J. Treble,** and T. E. Walsworth. 2025. Cyclical, multi-trophic-level responses to a volatile, introduced forage fish: learning from four decades of food web observation to inform management. Fisheries 50:52-65.

BACKGROUND

Rainbow Smelt *Osmerus mordax* are an important forage species for a variety of sport fish (Scott and Crossman 1973). Because of their desirable characteristics, Rainbow Smelt introduction has been used as a management tool to enhance fisheries and encourage sport fish growth (Evans and Loftus 1987; Mercado-Silva et al. 2006). Thus, Rainbow Smelt have spread from northeastern North America throughout the Great Lakes watershed and the West (Mercado-Silva et al. 2006). Although Rainbow Smelt introductions have been associated with increased growth of sport fish, they have also been associated with undesired food web changes (Mercado-Silva et al. 2007). For example, declines in Walleye recruitment and abundance have been associated with increasing Rainbow Smelt abundance (Schneider and Leach 1977; Johnson and Goettl 1999; Mercado-Silva et al. 2007) which may be a result of predation on (Lepak et al. 2023) and competition with young Walleye for prey resources (Johnson and Goettl 1999; Mercado-Silva et al. 2007; Lawson and Carpenter 2014). Further, Rainbow Smelt populations have the potential to exhibit self-regulated, cyclical patterns and alternating year-class dominance attributable in part to their cannibalistic behavior, making them a challenging and inconsistent forage on which to base a sport fishery (Hendersen and Nepszy 1989; He and LaBar 1994).

In 1983, Rainbow Smelt were introduced into Horsetooth Reservoir, Larimer County, Colorado to enhance Walleye and Smallmouth Bass growth (Goettl and Jones 1984). Historically, Horsetooth Reservoir was managed as a two-tiered fishery with naturally reproducing Walleye (rare in Colorado reservoirs) as a primary component along with stocked Rainbow Trout and kokanee salmon. The unique, naturally recruiting Walleye had been sustained largely on a forage base of Yellow Perch *Perca flavescens* which collapsed, and managers attempted to replace with Rainbow Smelt. Horsetooth Reservoir is the only reservoir in Colorado that supports Rainbow Smelt, and the population has fluctuated widely since their introduction. Because of the importance of the Walleye fishery and reliance on a volatile Rainbow Smelt population, Horsetooth Reservoir is a relatively data rich system with intermittent research and monitoring efforts focused on multiple ecosystem components. Over 40 years of data are available from this system, along with cyclical periods of high densities of Rainbow Smelt during 1987–1996 and since 2013. This time-series provided an opportunity to evaluate long-term, multi-trophic level responses to Rainbow Smelt abundance across two distinct periods. In this paper, we characterize community-level trophic interactions and population dynamics among Rainbow Smelt and other biota including Walleye, Mysis*,* and *Daphnia* spp. We used machine learning to identify the best predictors of poor Walleye recruitment based on information from historic and contemporary datasets spanning four decades. Repeated patterns in several ecosystem components along with empirical observations prompted us to hypothesize that indicators linked to Rainbow Smelt abundance would be the best predictors of poor Walleye recruitment. We hoped to identify indices that can inform and prepare fisheries managers for near-term impacts from Rainbow Smelt population dynamics in anticipation of taking actions such as stocking Walleye fry or fingerlings, increasing availability or quality of Walleye spawning habitat, altering Walleye harvest regulations, and limiting Rainbow Smelt access to their spawning habitat.

PUBLICATION ABSTRACT

Species introductions can have significant effects on recipient ecosystems. Anticipating potential ecosystem change in response to introduced species based on historical information can help managers prepare for future conditions. Rainbow Smelt *Osmerus mordax* have been introduced widely to improve sport fish growth. As intended, Walleye *Sander vitreus* growth in Horsetooth Reservoir, Colorado increased after Rainbow Smelt introduction, but poor Walleye recruitment occurred as well. Additionally, Opossum Shrimp *Mysis diluviana* became absent from both predator diets and intermittent surveys, the dominant *Daphnia* species in Horsetooth Reservoir shifted and *Daphnia* densities declined significantly. These patterns were repeated during two different time periods of increased Rainbow Smelt abundance, suggesting that Rainbow Smelt have a strong influence on multiple components of the ecosystem. The repetition of responses to Rainbow Smelt offered the opportunity to evaluate indicators to anticipate potential ecosystem regime shifts that restructure predator-prey dynamics across trophic levels. Three predictors (i.e., high estimated Rainbow Smelt abundance, high catch rates of large Walleye, and low *Daphnia* densities) were associated with poor Walleye recruitment. Simple indicators like these could inform timely management decisions to take advantage of the benefits Rainbow Smelt offer, while lessening their undesirable effects. For example, management decisions could be made, such as preparing for Walleye egg collections, rearing and stocking of Walleye, increasing availability or quality of Walleye spawning habitat, allowing more protective or liberalized adult Walleye harvest to promote natural recruitment, and limiting Rainbow Smelt access to their spawning habitat.

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RESEARCH PRIORITY: **Food webs and predator-prey interactions (Part 2):** Alternating ecosystem states driven by Rainbow Smelt densities in Horsetooth Reservoir.

OBJECTIVES

To identify potential mechanisms linking Walleye recruitment failure in Horsetooth Reservoir to Rainbow Smelt proliferation, and to prepare and submit a manuscript with our findings.

PUBLICATION

Walsworth, T. E., **A. G. Hansen,** and **J. M. Lepak.** 2025. Alternating ecosystem states driven by an invasive fish in a life history intraguild predation system. Canadian Journal of Fisheries and Aquatic Sciences 82:1-15.

BACKGROUND

Horsetooth Reservoir has supported a popular Walleye fishery since the 1950s, and Rainbow Smelt were introduced in 1983 to provide forage for the Walleye and Smallmouth Bass populations of the reservoir. Increasing abundance of Rainbow Smelt through the late 1980's and early 1990's drove major changes to Horsetooth Reservoir's fish community and food web structure (e.g., Johnson and Goettl 1999; Lepak et al. 2025). Rainbow Smelt compete with young Walleye for zooplankton prey, reducing the abundance of preferred *Daphnia* spp. (Lepak et al. 2025), and prey upon age-0 Walleye (Lepak et al. 2023). However, larger Walleye prey heavily on Rainbow Smelt and demonstrate elevated growth rates and greater abundance when Rainbow Smelt are abundant (Lepak et al. 2025). Thus, Rainbow Smelt have distinct and divergent impacts on different size-classes of Walleye, and cyclic dynamics of Rainbow Smelt abundance have occurred alongside alternating periods of low recruitment, high adult abundance and high recruitment with low adult abundance for Walleye in Horsetooth Reservoir (Lepak et al. 2025). These two states provide very different fishery values and present fisheries management trade-offs (lack of recruitment with abundant quality-sized fish vs. consistent recruitment with rare quality-sized fish). Understanding how recruitment, growth and survival of Walleye are impacted by cyclic food web dynamics may inform future management efforts aiming to maintain recreational fishery values.

We developed a time-varying stage-structured population model characterized by a binary latent ecosystem state to disentangle cyclic dynamics observed across multiple trophic levels. We analyze data from three trophic levels and multiple life-stages in the aquatic community of Horsetooth Reservoir collected across 42 years. Specifically, we examine (1) how changes in abundance at lower trophic levels affect the vital rates of different life stages of Walleye, (2) whether latent changes in ecosystem state can drive cyclic dynamics across life-stages of Walleye, and (3) how observations of lower trophic levels can be used to predict the current state of the ecosystem and therefore how we would expect the Walleye population to change. The results of our work are broadly relevant to understanding the population dynamics of size, stage, or age-structured populations experiencing non-stationary ecosystem conditions, and can directly inform the management of the fishery in Horsetooth Reservoir.

PUBLICATION ABSTRACT

Prey species that compete with or consume early-life stages of their primary predator (i.e., life-history intraguild predation (LHIGP)) can generate alternate ecosystem states and distinct shifts in predator demographics. Identifying ecological conditions underlying alternate states can inform adaptive management of LHIGP-driven ecosystems and fisheries. We developed a time-varying, stage-structured population modeling framework to explore the dynamics of a walleye (*Sander vitreus*) population supported by invasive rainbow smelt (*Osmerus mordax*), a widely introduced forage fish that can negatively affect walleye recruitment. Our model identified two distinct and cyclic states over a 42-year time-series. The first was characterized by low smelt abundance, elevated *Daphnia* density and walleye recruitment, but poor walleye growth and survival to larger size, while inverse patterns characterized the second state. Strong state-dependent shifts in predator vital rates and population structure emphasized the need for flexible management approaches (e.g., stocking, harvest regulations) to maintain fisheries quality and population sustainability. Our modeling framework is broadly applicable to understanding the dynamic nature and informing adaptive management of nonstationary systems, such as those characterized by LHIGP.

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<u>RESEARCH PRIORITY</u>: **Food webs and predator-prey interactions (Part 3):** The role of Rainbow Smelt cannibalism versus Walleye predation for controlling Rainbow Smelt densities in Horsetooth Reservoir.

OBJECTIVES

To better understand 1) the role of predation by Walleye versus cannibalism as controls of the Rainbow Smelt population in Horsetooth Reservoir, an ecosystem driven by reciprocal life-history intraguild predation dynamics, and 2) the potential for a more diverse set of predators to enhance the stability of the forage base.

BACKGROUND

Horsetooth Reservoir supports an important and unique fishery on the Colorado landscape. Walleye are generally considered top predators in the system, and a cyclic population (also described as "boom-bust") of Rainbow Smelt are their prey when available (Lepak et al. 2025). This fishery is unique as the only sport fishery supported by Rainbow Smelt in Colorado despite smelt introductions in multiple systems from 1983 to 1993. The naturally reproducing Walleye in Horsetooth Reservoir experienced increased growth rates as a result of the Rainbow Smelt introduction there in 1983 (Johnson and Goettl 1999). However, periods of high Rainbow Smelt abundance also correspond with periods of exceptionally poor Walleye recruitment and the need to supplement the population by stocking (Johnson and Goettl 1999; Lepak et al. 2025; Walsworth et al. 2025).

The predator-prey dynamics between Walleye and Rainbow Smelt in Horsetooth Reservoir are complex, and driven by what is known as intraguild predation. This phenomenon formally known as life history intraguild predation (LHIGP) occurs when an organism that is generally considered a competitor with another species at a given size or life stage can consume that species at a different point during their life history because of ontogenetic shifts resulting from growth or metamorphosis (Polis and Holt 1989, 1992; Holt and Polis 1997; Abrams 2011; Toscano et al. 2016). In fisheries, large predators often begin life as small individuals competing for food resources with a variety of species, including those that might be considered prey later in life after the predator experiences growth and ontogenetic shifts, and these interactions are examples of LHIGP (van de Wolfshaar et al. 2006). In the case of Horsetooth Reservoir, young-of-year Rainbow Smelt compete with juvenile Walleye for food resources, but as adults, Walleye consume Rainbow Smelt (Johnson and Goettl 1999). However, as Rainbow Smelt grow larger, they can also become piscivorous, capable of consuming young Walleye that are generally considered Rainbow Smelt predators (Lepak et al. 2023). Because Walleye and Rainbow Smelt can both compete for resources and consume each other, LHIGP in Horsetooth Reservoir is considered reciprocal LHIGP (Montserrat et al. 2012).

Systems that are driven by LHIGP dynamics are theorized to fall within three categories including coexistence, exclusionary, and alternative stable states (Polis and Holt 1989, 1992; Holt and Polis 1997). Stable coexistence is considered rare, and factors like predator-prey interactions, system productivity, and population demographics must be balanced such that one species does not outcompete the other species for forage when they are young (Holt and Polis 1997; Abrams 2011; Hin et al. 2011; Toscano et al. 2016). Commonly in fisheries, the species that attains a larger ultimate size is unable to effectively compete for the limiting shared prey resource when they are young, leading to the eventual exclusion of the larger species (van de Wolfshaar et al. 2006). Additionally, there is potential for LHIGP dynamics to result in alternate stable states where species demographics, behaviors, and/or interactions shift, but may remain relatively constant until a transition into another stable state (Walsworth et al. 2025). Within this predator-prey dynamic, cannibalism can also be an important component that moderates species densities and subsequent competitive interactions (Montserrat et al. 2012; Byström et al. 2013; Toscano et al. 2016, 2017). Although compelling, theoretical models related to LHIGP are largely based on simple invertebrate or amphibian experimental communities at small scales (Abrams 2011; Hin et al. 2011; Toscano et al. 2016). Thus, more empirically-based research at full system scales could inform, and potentially reconcile, discrepancies between LHIGP theory (i.e., the prevalence of coexistence when theory generally supports exclusion) and observations on the landscape.

Understanding and potentially controlling Rainbow Smelt competition with, and predation upon, juvenile Walleye is important for fisheries management in Horsetooth Reservoir. Others have observed poor Walleye recruitment in conjunction with dense populations of forage fish including Rainbow Smelt (e.g., Mercado-Silva et al. 2007), and efforts have been made to stock predators (e.g., Walleye) in high enough numbers to control forage fish densities. For example, Rudstam et al. (2011) increased Walleye stocking rates in Cayuta Lake (Schuyler County, New York, USA) to disadvantage Alewife *Alosa pseudoharengus*, an effective zooplanktivore. Although Alewife numbers declined, Alewife recruitment was not diminished, and the authors suggest compensatory responses in cannibalism and recruitment should be considered when attempting to manipulate a forage base. Based on the findings of others and four decades of observation in Horsetooth Reservoir, we are interested in the relative importance of Walleye predation versus Rainbow Smelt cannibalism for controlling the biomass of Rainbow Smelt. We are also interested in the potential for the Rainbow Smelt population to remain more stable and support a more diverse suite of predators.

PROJECT PROGRESS

Study Site

Horsetooth Reservoir represents a well-studied system where Walleye are a popular target for recreational anglers, and a relatively dense population of Rainbow Smelt currently exists. Young-of-year Walleye and Rainbow Smelt compete for zooplankton resources, and two periods of high Rainbow Smelt density have corresponded to poor Walleye recruitment in Horsetooth Reservoir (Johnson and Goettl 1999; Lepak et al. 2025; Walsworth et al. 2025). Both species are capable of consuming juvenile stages of the other species (reciprocal LHIGP), and adult Walleye often focus on Rainbow Smelt as prey (Johnson and Goettl 1999). Furthermore, Rainbow Smelt have been found to be highly cannibalistic in Horsetooth Reservoir, with the majority of adult Rainbow Smelt diets consisting of juvenile Rainbow Smelt in some years (Lepak et al. 2025).

These interactions drive observed patterns in Walleye recruitment and growth, and provide the opportunity to evaluate predator-prey interactions within a reciprocal LHIGP context.

Methods

To explore fisheries management questions within Horsetooth Reservoir, we will use Walleye and Rainbow Smelt bioenergetics modeling informed with empirical data from Horsetooth Reservoir. We will couple what is gained from individual-based bioenergetics models with information about the Walleye and Rainbow Smelt populations in Horsetooth Reservoir to determine overall predation pressure on Rainbow Smelt and the potential for Rainbow Smelt population control. Currently, individual-based bioenergetics simulations are complete for male and female Walleye and Rainbow Smelt in Horsetooth Reservoir. Results from the individual based simulations will be coupled with population-level information to scale findings up to the community level to compare the importance of Walleye predation and Rainbow Smelt cannibalism in Horsetooth Reservoir. These findings will help us determine if Rainbow Smelt control by Walleye is feasible, and if more predator biomass might be supported by the Rainbow Smelt population. A manuscript is being developed that will describe our results.

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RESEARCH PRIORITY: **Rapid response to the discovery of Bighead Carp *Hypophthalmichthys nobilis* in Jack B. Tomlinson Pond, Colorado:** Reproduction, survival, growth, and maximum age of Bighead Carp.

OBJECTIVES

We were asked to provide evidence to support the hypothesis that Bighead Carp were not reproducing naturally in Colorado, and to provide information in the form of a peer-reviewed manuscript to the invasive species research community to better understand Bighead Carp, their survival, growth, and maximum lifespan.

PUBLICATION

Lepak, J. M., A. G. Hansen, T. L. Martinez, E. A. Stewart, D. J. Pinkus, A. M. Pelletier, and **A. J. Treble.** 2025. Maximum age of Bighead Carp *Hypophthalmichthys nobilis* exceeds 30 years: implications for anticipating invasive species establishment and impacts. Journal of Fish Biology 2025:1-8. DOI: 10.1111/jfb.70181.

BACKGROUND

Invasive species have the potential to cause widespread and undesirable ecological and economic impacts on ecosystems (Simberloff 2011). Invasive Bighead Carp have spread throughout the Mississippi River Basin (USA), negatively impacting ecosystems, yet relatively little is known about them. Risk assessments have predicted that invasive carp could have significant ecological and economic impacts on important fisheries in a variety of freshwater systems (Kolar et al. 2007; Rutherford et al. 2021). However, there are many challenges associated with predicting if an invasive species will become established and quantifying future deleterious ecological and economic impacts. Despite challenges, predictive models and scenarios are necessary to prepare for, and potentially address, invasive carp and associated costs to fisheries, recreation, and commercial interests estimated in the hundreds of millions to billions USD (Cooke and Hill 2010; Lauber et al. 2016, 2020; Zhang et al. 2016). Minimizing sources of error in model inputs in the context of prevention and control costs and ecological and economic impacts can be crucial to inform management and decision making.

In the case of Bighead Carp, Birdsall et al. (2024) describe the need for further validation and description of age and growth determination, noting that age interpretation for these species is particularly challenging. No standard hard structure or approach has been selected for age interpretation, and few authors (prior to Birdsall et al. 2024) have formally addressed precision or hard structure comparisons in Bighead Carp. Our objective was to add to what is known about Bighead Carp age interpretation (see Birdsall et al. 2024) using information from a remnant cohort of Bighead Carp captured 32 years after they were stocked in a small pond near Denver, Colorado (USA). We also hoped to expand upon what is known about Bighead Carp age, growth, and habitat requirements in a unique system beyond their invasion front in western Nebraska in the South Platte River near the border of Colorado.

PUBLICATION ABSTRACT

Invasive Bighead Carp *Hypophthalmichthys nobilis* have spread throughout the Mississippi River Basin, negatively impacting ecosystems. We used a remnant population (32 years after stocking) to better understand Bighead Carp. We observed high annual survival (>95%), but growth was relatively slow. Lapilli otolith sections were reliable aging structures, but underestimated Bighead Carp age by ~ 10%. Dorsal fin rays and postcleithra also showed some promise for age interpretation. This study provides information about exceptionally old Bighead Carp, with unique survival, growth, and habitat conditions that could further inform invasion models.

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RESEARCH PRIORITY: **Informing Walleye harvest management:** Model evaluation of alternative length-based harvest regulations for Pueblo Reservoir Walleye.

OBJECTIVES

Integrate angler dynamics from creel surveys and Walleye population demographics from fisheries-independent surveys into a general modeling framework to explore alternative harvest strategies for broodstock in Pueblo Reservoir and potentially other waterbodies. Prepare a manuscript with findings and submit to a peer-reviewed journal for publication.

MANUSCRIPT IN PREPARATION

Hansen, A. G., C. Tucker, and **J. M. Lepak.** Exploiting sexually dimorphic growth to improve wild broodstock management of a popular sport fish. In preparation for Fisheries Management and Ecology.

BACKGROUND

Walleye are highly sought sport and food fish in eastern Colorado. 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 fingerlings later in May or early June. Statewide stocking requests are supported through spring egg-collection operations from wild broodstocks in three primary reservoirs: Chatfield, Cherry Creek and Pueblo. Harvest regulations (18-inch minimum length limit [MLL]; daily bag limit = 3-5 depending on reservoir; only one >21 inches allowed) on each broodstock reservoir are restrictive to protect larger females essential for meeting egg-collection goals and statewide stocking schedules. However, anglers have long expressed interest in relaxing regulations at Pueblo Reservoir to allow harvest of fish <18 inches. The 18-inch MLL was put in place in 1993 following a period of liberalized regulations (daily bag limit of 10 fish with no size restrictions) that led to overexploitation of broodstock. Since implementation of the 18-inch MLL, various regulation changes have been proposed by anglers and discussed at round tables, but never granted. A new research project was initiated in 2018 utilizing standard fisheries survey, analysis and modeling techniques (not used previously) to objectively compare potential population responses to alternative harvest regulations and better inform management decisions.

MANUSCRIPT DRAFT

Journal: Fisheries Management and Ecology

Exploiting sexually dimorphic growth to improve wild broodstock management of a popular sport fish

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1 | INTRODUCTION

Inland recreational fisheries provide social, cultural, and economic benefits, and contribute to food security (Lynch et al., 2016, 2024; Parisek et al., 2024). Freshwater recreational fisheries are typically open-access and require adaptive management systems that promote resilience to unregulated angling effort, exploitation, and environmental change to maintain fishery benefits (Post et al., 2002; Post, 2013). Managers have long utilized input (e.g., seasonal closures) and output controls (e.g., length-based harvest limits) to protect from overfishing and population declines (Noble & Jones, 1999; Radomski et al., 2001). However, changing social-ecological values, shifts in fisheries demographics or supporting ecosystems, or advancements in regulation science may warrant or necessitate deviation from traditional strategies to balance angler preferences, management needs, and requirements for sustainability (Johnston et al., 2010; Sass, 2025).

The utility of output controls is varied. Combined bag and length-based harvest limits can be designed to manipulate population size structure for meeting angler expectations (Noble & Jones, 1999), achieving maximum sustainable yield (Beverton & Holt, 1957), or to prevent recruitment overfishing. The latter is when exploitation reduces the numbers of fish reaching reproductive age and/or numbers of mature adults to a point where the stock can no longer sustain itself. To safeguard against recruitment overfishing, minimum length limits (MLL) have been traditionally used where fish smaller than the MLL (usually sexually immature) must be released, but fish above the MLL (usually sexually mature) may be harvested (Allen et al., 2013). Theoretical models demonstrate that MLLs maximize stock biomass production and yield while supporting recruitment to reproductive size, allowing fish to “spawn at least once” before being vulnerable to harvest, thereby maintaining population replacement despite harvest of mature adults (Arlinghaus et al., 2010; Gwinn et al., 2015).

Concentrating harvest on mature adults has become increasingly scrutinized (Birkeland & Dayton, 2005; Ahrens et al., 2020). Counter to intentions, under intensive fishing efforts, MLLs can lead to truncation of population size/age structure, degradation of spawning stock, and reduced recruitment (Sanchez-Hernandez et al., 2016; Flink et al., 2024). Through maternal effects (Venturelli et al., 2010) or hyperallometric scaling of fecundity (Barneche et al., 2018), the reproductive value of larger (older) females can be high. As a result, larger females may contribute disproportionately to recruitment and drive stock productivity (Arlinghaus et al., 2010; Shaw et al., 2018). Further, MLLs and size/age truncation may not align with angler preferences. Many anglers see large fish as memorable trophies rather than providing consumptive value (Jacobson, 1996; Arlinghaus, 2006). Consumptive-oriented anglers may prefer smaller “pan-sized” fish, where the number harvested instead of biomass yield is more important. Harvest opportunity may be reduced if MLLs exceed lengths considered pan-size or are most vulnerable to catch by anglers. These situations could result in waste and the potential for recruitment overfishing if hooking mortality is high (Coggins et al., 2007). Lastly, MLLs could be misaligned when applied to fisheries where the bioaccumulation of contaminants is a concern for larger, older adults (Johnson et al., 2015).

The potential drawbacks of MLLs have motivated assessment of non-traditional strategies in the form of harvest slot limits (HSL). HSLs protect small and large fish but allow take of intermediate-sized fish within a specified window. Models have demonstrated the ability of HSLs to outperform MLLs by supporting greater numerical harvest, catches of trophy fish, and reduced waste while maintaining reproductive biomass across a range of exploitation rates and life history strategies (Arlinghaus et al., 2010; Gwinn et al., 2015; Ahrens et al., 2019). However, models have only considered dynamics under natural reproduction and an assumed stock-recruitment relationship. In regions where reproduction is limited, populations are sustained through annual stocking. Eggs are manually collected/fertilized from wild broodstock and raised in hatcheries to support landscape-level stocking schedules (Koupal et al., 2015; Blackwell et al. 2018). In this context, management priority is to maintain sufficient numbers of mature adults for consistent and efficient egg collection. Population declines could place broader fisheries systems at risk. Therefore, managers may apply special protective regulations to wild broodstock, such as higher than normal MLLs. However, given the potential for HSLs to promote more natural size/age structures and provide added protection for mature adults, recreational broodstock fisheries may benefit from their application. Added protections from HSLs may reduce variability/uncertainty in annual egg collections driven by dynamic angler effort responses under MLLs that concentrate harvest on broodstock (Allen et al., 2013).

Studies comparing the efficacy of HSLs to MLLs in the context of wild broodstock management are lacking. Here, a population model was used to simulate the effects of each regulation on equilibrium population size/age structure, total egg production, and the composition of mortality under constant recruitment (i.e., annual stocking). The model was constructed and calibrated using data from walleye (*Sander vitreus*) broodstock populations. Walleye are a highly valued and widely introduced North American species for which anglers tend to be harvest-oriented (Baccante & Colby, 1996; Fayram, 2003). In the United States, wild broodstock are used to stock over one billion walleye annually (Halverson, 2008). Because walleye also exhibit sexually dimorphic growth, where females achieve larger body sizes on average than males, interactions among population demographics, angler behavior, and length limits could mediate regulation efficacy in more complex ways (Wszola et al., 2022) than expected from equal growth, as assumed in previous modeling studies (Gwinn et al., 2015). For example, relationships among sex-dependent growth and length limits may create biologically relevant differences in the probability of being legal size at a given age between males and females, resulting in divergent responses to harvest and implications for egg production. The specific objectives of modeling were to determine if non-traditional HSLs could outperform traditional MLLs for managing wild broodstocks comprised of sexually dimorphic individuals and to evaluate the sensitivity of egg production to stocking success, angler catch efficiency (i.e., catchability), and angler effort under each regulation.

2 | METHODS

2.1 | Study Region and Systems

Within the Great Plains region of the United States, walleye fisheries are largely sustained through hatchery propagation of fertilized eggs from wild broodstock as systems can support high exploitation rates (Quist et al., 2010; Koupal et al., 2015; Blackwell et al., 2018; Zebro et al., 2025). Colorado relies on three primary broodstock systems (Chatfield, Cherry Creek, and Pueblo reservoirs) to support the stocking of 35-64 million walleye fry and fingerlings into 24-41 waterbodies annually. Walleye demographics in Chatfield (surface area [SA] at full conservation pool = 578.7 ha; max. depth = 15.2 m; mean depth = 7.4 m; elevation = 1655.7 m), Cherry Creek (344.0 ha; 9.1 m; 4.8 m; 1691.6 m), and Pueblo (1802.1 ha; 21.0 m; 7.3 m; 1487.5 m) were jointly used to inform the population model given similarities in walleye growth and maturation. A restrictive MLL (457 mm total length [TL]) and daily bag limit (3-5 fish; only one may be >533 mm TL) are currently in place on each reservoir.

2.2 | Population Demographics

Fall Walleye Index Netting (FWIN; Morgan, 2002; Giacomini et al., 2020) was conducted on Chatfield (October 28-30, 2019; *n* = 14 gangs), Cherry Creek (October 23-25, 2019; *n* = 12 gangs) and Pueblo (October 29-November 1, 2018; *n* = 16 gangs). All walleye captured were measured for TL and weighed (WW; nearest g). Sagittal otoliths were collected from all or a systematic random subsample of fish for age, growth, maturity and mortality estimation. Sex and maturity status were classified from visual examination of gonads (Duffy et al., 2000). Otolith samples were supplemented by incidental mortalities during spring egg collections from each broodstock over 2018-2024. Most walleye encountered during egg collections at Pueblo Reservoir were sexed externally and measured for TL in 2017 (*n* = 1320), 2018 (*n* = 1262), 2022 (*n* = 1508), and 2023 (*n* = 1120) to characterize broodstock size-structure. Broodstock were collected with 61.0-m-long × 1.8 m high multifilament gill nets (76 mm stretch mesh).

2.2.1 | *Age, growth, maturity and fecundity*

Left sagittal otoliths were embedded in clear epoxy resin (West System 105) and sectioned (thickness = 0.58 mm) transversely through the core with an IsoMet low-speed precision saw (Buehler). Otolith sections were coated with mineral oil and aged (a) independently by two experienced readers through a dissecting microscope using transmitted light at 30–50× magnification. Readers convened to reach consensus on age estimates that disagreed. The outer edge of each otolith from fall-captured fish (FWIN) was counted as an annulus. Therefore, fall ages reflected what each fish would have been the following spring to align with otoliths from incidental mortalities during spring egg collections. This approach assumed that most growth occurred over summer and fall (Quist et al., 2002). Sex-dependent (g; female or male) mean TL-at-age ($TL_{a,g}$) was expressed using a von Bertalanffy growth function (vBGF):

$$TL_{a,g} = TL_{\infty,g} \cdot \left(1 - e^{-K_g \cdot (a - a_{0,g})}\right) \cdot e^{\varepsilon_g}$$

where $TL_{\infty,g}$ = mean asymptotic TL, K_g = instantaneous growth rate coefficient, $a_{0,g}$ = hypothetical age at zero length, and e^{ε_g} is the multiplicative error term in which $\varepsilon_g \sim N(0, \sigma_g)$ and σ_g = residual standard error. Parameters were estimated by fitting the vBGF to *log*(TL) and *log*(*a*) observations from individual fish across broodstocks (*n* = 826 females, *n* = 1180 males; Table 1; Figure 1A) using the 'nls' function within the 'stats' package in R (Ogle, 2016; R Core Team, 2025). Mean WW-at-age ($WW_{a,g}$) was a function of $TL_{a,g}$. Separate functions were used for small (<600 mm TL) and large fish (≥600 mm TL; subscript 'size') since a single function could not reconcile WW measurements from larger walleye:

$$log(WW_{a,g}) = log(A_{size}) + B_{size} \cdot log(TL_{a,g}) + \varepsilon_{size}$$

Parameters (A_{size} and B_{size}) were estimated by fitting to individual measurements across broodstocks from FWIN captured fish (sexes combined; *n* = 1479 for small and *n* = 36 for large size-groups) using the 'lm' function in R (Table 1; Figure 1B). A bias correction factor ($c_{WW,size} = e^{(\frac{\sigma^2_{size}}{2})}$) was used when back-transforming $WW_{a,g}$ from *log* space (Ogle, 2016). Sex-dependent probability of maturity-at-age ($p_{mat,a,g}$) was a logistic function of $TL_{a,g}$:

$$p_{mat,a,g} = \frac{e^{\beta_{0,g} + \beta_{1,g} \cdot TL_{a,g}}}{1 + e^{\beta_{0,g} + \beta_{1,g} \cdot TL_{a,g}}}$$

Parameters ($\beta_{0,g}$ and $\beta_{1,g}$) were estimated using logistic regression fit to individual observations (immature = 0, mature = 1; *n* = 824 for females, *n* = 1182 for males) across broodstocks with the 'glm' function (family = 'binomial') in R (Ogle, 2016; Table 1; Figure 1C). Mean fecundity-at-age (f_a) was a function of $TL_{a,female}$:

$$f_a = \alpha \cdot {TL_{a,female}}^{\beta}$$

Parameters (α and β) were derived for female walleye from Pueblo Reservoir by linking TL measurements recorded during 2018 spring egg collections to the hatchery-derived estimate of total eggs (~41 million). Of the 831 females encountered, 610 were spawned. Lengths of 610 females were simulated from a lognormal distribution with mean (505 mm) and SD (67 mm) derived from the sample of 831 to approximate TLs of the spawned subset. Fecundity was predicted for each simulated TL and values for α and β were found such that predicted eggs summed across females = the hatchery estimate (Table 1).

2.2.2 | *Abundance and mortality*

The population model was calibrated using estimates of walleye density, annual mortality, and angler harvest from Pueblo Reservoir. Mark-recapture estimates of abundance for adult walleye (≥450 mm TL) in Chatfield (low density population; 2.91 adults/ha; 95% confidence limit [CI] = 1.18-7.27) and Cherry Creek (high density; 16.69 adults/ha; 95% CI = 11.40-25.44) were used to calibrate FWIN gill net catchability to Colorado reservoirs. Catchability was similar between systems despite large differences in adult density, supporting application of this approach (Hansen et al., 2023). The high-density gill net catchability coefficient estimated from Cherry Creek ($q_{FWIN,CCreek}$ = 0.203 ha/gang; 95% CI = 0.133-0.298) was applied to the depth-strata area- (ha within 2-5 and 5-15 m depths) and effort-weighted (gangs set within each strata) catch-per-unit-effort of walleye ≥457 mm TL in Pueblo ($CPUE_{FWIN,Pueblo}$; fish/gang) to estimate the density ($D_{FWIN,Pueblo}$) of adults vulnerable to angler harvest:

$$D_{FWIN,Pueblo} = \frac{CPUE_{FWIN,Pueblo}}{q_{FWIN,CCreek}}$$

$D_{FWIN,Pueblo}$ was expanded to an abundance ($N_{FWIN,Pueblo}$) based on reservoir surface area at the time of FWIN (1552 ha) and partitioned by sex ($N_{FWIN,Pueblo,g}$) using relative proportions of fish ≥457 mm TL (fully vulnerable to multifilament gill nets; 0.90 for females, 0.10 for males) encountered during 2018 spring egg collections.

A joint age-length-key was constructed for each sex by combining samples across broodstocks. The key was applied to sex-specific catches from the 2017, 2018, 2022, and 2023 spring egg collections on Pueblo Reservoir to estimate catch-at-age. Weighted catch-curve regression was used to estimate total instantaneous mortality (Z_g) and annual survival ($S_g = e^{-Z_g}$) by sex and year. Descending limbs were defined as ages following peak catch-at-age (≥age-6 for all cases; Ogle, 2016). Regressions were implemented using the 'catchCurve' function within the 'FSA' package in R (Ogle, 2025). Rates were averaged across years ($\bar{Z}_g, \bar{S}_g$) by sex (Table 1).

Creel surveys were conducted on Pueblo Reservoir in 1987, 1989, 1991, 1993, 1994, 2012, and 2021. The 2021 survey (April—October) was used to estimate contemporary fishing effort (angler-days by month), catch (number and rate [fish/angler-day] by month) and harvest (legal-sized fish ≥457 mm retained by month). Survey-design and analytical procedures followed Colorado standards (Schisler & Bowden, 2021). One clerk counted boat and shore anglers across the reservoir from a jet-propelled personal watercraft (PWC) at three designated times (0800h, 1200h, and 1600h) on one randomly selected weekday and one weekend day each week. Between counts, the PWC clerk interviewed shore anglers. Additional clerks were stationed at boat ramps to interview boat anglers who had completed trips.

Estimated harvest ($H_{Creel,2021}$) over April—October (predominant walleye fishing season) was used to separate $\bar{Z}_g$ into fishing ($\bar{F}_g$) and natural ($\bar{M}_g$) mortality (Slipke & Maceina, 2013). Age classes in catch-curve regressions aligned with those most vulnerable to harvest under the 457 mm MLL. Because $N_{FWIN,Pueblo}$ reflected a post-harvest estimate, exploitation rate (μ) was:

$$\mu = \frac{H_{Creel,2021}}{(N_{FWIN,Pueblo} + H_{Creel,2021})}$$

It was assumed that both sexes experienced the same μ when computing F_g and M_g:

$$\bar{F}_g = \mu \cdot \bar{Z}_g / (1 - \bar{S}_g)$$

$$\bar{M}_g = \bar{Z}_g - \bar{F}_g$$

2.3 | Population Model and Outputs

The model simulated monthly (time-step denoted by t) and sex-dependent equilibrium numbers-at-age ($N_{a,t,g}$; 0.083 year increments) using demographic rates computed for an average-sized individual within each age-class:

$$N_{a+0.083,t+1,g} = N_{a,t,g} - H_{a,t,g} - NM_{a,t,g}, for\ 1 \leq a \leq a_{max}$$

where $H_{a,t,g}$ = numbers harvested, $NM_{a,t,g}$ = natural mortalities, and a_{max} = maximum effective age of walleye (i.e., readily encountered during routine sampling efforts). A monthly time step was used to account for seasonality in fishing effort and catch rate, which helped clarify the potential effect of daily bag limits. Recruitment ($N_{1,t,g}$) was driven by annual stocking:

$$N_{1,t,g} = 0.5 \cdot N_{fry} \cdot S_{fry}$$

where N_{fry} = number of age-0 walleye fry stocked and S_{fry} = survival rate from stocking (typically in April) to March of the following year. Therefore, each “full-age” time-step occurred in March, which aligned with the onset of egg collection operations. The simplified recruitment function assumed that sufficient eggs could be collected from emergency broodstocks or obtained through other means (e.g., egg trades) to fully stock each year.

Joint numbers lost to harvest or natural mortality ($HNM_{a,t,g}$) were determined by combining probabilities of angler capture ($cp_{a,t,g}$), being of legal size given a capture ($lp_{a,t,g}$; 0 if catch-and-release), being retained within the daily bag limit given a legal capture ($rp_{a,t}$; 1 if no limit), and natural death in the absence of harvest mortality ($nm_{a,t,g}$). Harvest probability ($hp_{a,t,g}$) in the absence of natural mortality was:

$$hp_{a,t,g} = cp_{a,t,g} \cdot lp_{a,t,g} \cdot rp_{a,t}$$

When occurring simultaneously, harvest and natural deaths were competing sources of mortality:

$$HNM_{a,t,g} = N_{a,t,g} \cdot \left(hp_{a,t,g} + nm_{a,t,g} - \left(hp_{a,t,g} \cdot nm_{a,t,g}\right)\right)$$

Numbers for $HNM_{a,t,g}$ were parsed into $H_{a,t,g}$ and $NM_{a,t,g}$ proportionately, where:

$$H_{a,t,g} = HNM_{a,t,g} \cdot \left(hp_{a,t,g}/\left(hp_{a,t,g} + nm_{a,t,g}\right)\right)$$

and:

$$NM_{a,t,g} = HNM_{a,t,g} - H_{a,t,g}$$

For non-zero $hp_{a,t,g}$, angler catches ($C_{a,t,g}$) were:

$$C_{a,t,g} = H_{a,t,g}/(lp_{a,t,g} \cdot rp_{a,t})$$

For cases in which $hp_{a,t,g} = 0$, catches and natural mortalities were governed by $cp_{a,t,g}$ and $nm_{a,t,g}$ (i.e., non-competing). Computation of $cp_{a,t,g}$ included components that depended on the specific month in which the time-step was associated (denoted by {*i*}; integer from 1 [January] to 12 [December]):

$$cp_{a,t,g} = q \cdot E \cdot P_{t\{i\}}^{boats} \cdot V_{t\{i\}}^{cr} \cdot V_{a,t,g}^{TL}$$

where q = fully-selected angler catchability coefficient (angler-day^{-1}), E = annual boat-angling effort (total boat-angler days) proportioned by month ($P_{t\{i\}}^{boats}$), $V_{t\{i\}}^{cr}$ = seasonal vulnerability of walleye to capture (values between 0 and 1), and $V_{a,t,g}^{TL}$ = size-dependent vulnerability of walleye to capture.

Bag limits (*BL*; legal fish allowed/angler-day) were simulated by computing the total daily angler catch potential of legal-sized fish (sexes combined; $CPUE_{legal,t}$) and scaling $rp_{a,t}$ based on the ratio of *BL* to $CPUE_{legal,t}$:

$$CPUE_{legal,t} = \frac{\sum_{a=1}^{a_{max}} N_{a,t,g} \cdot cp_{a,t,g} \cdot lp_{a,t,g}}{E \cdot P_{t\{i\}}^{boats}}$$

$$rp_{a,t} = \begin{cases} 1\ if\ CPUE_{legal,t} \leq BL \\ \dfrac{BL}{CPUE_{legal,t}} if CPUE_{legal,t} > BL \end{cases}$$

Model outputs included the adult density of age-3+ walleye in March (sexes combined), annual catches, harvests, and natural mortalities parsed by sex, total numbers of mature females and males present in March (i.e., available to egg collection operations), and total female spawn potential (*SP*; millions of eggs). Numbers of mature fish-at-age ($NMAT_{a,t\{i=3\},g}$) were derived from probabilities of maturity ($p_{mat,a,t\{i=3\},g}$):

$$NMAT_{a,t\{i=3\},g} = N_{a,t\{i=3\},g} \cdot p_{mat,a,t\{i=3\},g}$$

and SP from $NMAT_{a,t\{i=3\},female}$ and f_a:

$$SP_{t\{i=3\},female} = \left(\sum_{a=1}^{a_{max}} NMAT_{a,t\{i=3\},female} \cdot f_a\right)/1{,}000{,}000$$

2.4 | Model Parameterization and Calibration

Boat inspection data from Colorado’s Aquatic Nuisance Species (ANS) Program spanning 2012-2018 informed$P_{t\{i\}}^{boats}$. Boats were inspected for ANS and classified prior to launch, including during months outside the April–October creel period. Counts of classified fishing boats were summed by month and year, and proportions of counts by month were averaged across years (Figure 1D). Creel survey data informed $V_{t\{i\}}^{cr}$. Monthly catch rates of walleye (all sizes) were scaled to the maximum rate by year, then averaged by month across years. It was assumed that $V_{t\{i\}}^{cr}$ remained stable after October through March when creel data were absent (Figure 1E). Data extracted from Myers et al. (2014) informed $V_{a,t,g}^{TL}$. Myers et al. (2014) estimated size- and sex-dependent angler selectivity for walleye from tagging studies in Wisconsin, USA, lakes, and one lake (Big Sand) in Minnesota. Selectivity from Big Sand was most relevant to broodstocks in Colorado based on walleye age-and-growth (Jacobson, 1994). Selectivity values were extracted using WebPlotDigitizer (accessed November 11, 2025 at: https://automeris.io; version 5.2) and characterized using joint Gaussian functions limited to maximum observed values ($sel_{max,g}$; females = 1, males = 0.836):

$$V_{a,t,g}^{TL} = min(sel_{max,g}, e^{-\left(TL_{a,t,g}-TL_{1,g}\right)^2/\left(2\cdot k_{1,g}^2\right)} + \varphi_g \cdot e^{-\left(TL_{a,t,g}-TL_{2,g}\right)^2/\left(2\cdot k_{2,g}^2\right)} + \varepsilon_g)$$

Parameters ($TL_{1,g}$, $TL_{2,g}$, $k_{1,g}$, $k_{2,g}$,φ_g) were fit using ‘mle2’ within the ‘bbmle’ package (Bolker, 2022) in R (Table 1). Myers et al. (2014) found a significant catch-bias against male walleye in size-dependent angler selectivity, which was reflected in the fitted functions (Figure 1F). Peak selectivity aligned with the sizes of captured walleye most often reported by anglers during creel surveys in which a 457 mm MLL was in place.

Values for $lp_{a,t,g}$ were estimated by simulating 10,000 TLs-at-age for each sex from the vBGFs by generating random deviates from the multiplicative error terms. Legal-sized fish were tabulated for each regulation and divided by 10,000 (Smith et al., 2022). Five regulations were examined (Figure 2). A 305 mm MLL was simulated to reflect conditions on Pueblo Reservoir prior to 1993, in which no size restrictions and a BL of 10 walleye were in place (retention of walleye <305 mm was negligible; McGree, 2012). A 381 mm MLL regulates non-broodstock waters in Colorado (standard BL = 5 walleye). A 457 mm MLL regulates broodstock waters (BL on Pueblo Reservoir = 5 walleye). A narrow 381-457 mm HSL (BL = 5 walleye) was selected to balance protection of small and large walleye, incorporate familiar end-points from Colorado regulations, and align with peak size-dependent angler selectivity (Figure 1F). A wide 381-508 mm HSL was simulated for comparison. The wide HSL was implemented in another Great Plains walleye broodstock reservoir (Koupal et al., 2015).

Separate mortality schedules were used for model calibration versus simulation. Total mortality was used to back-calculate equilibrium age-1 recruits and S_{fry}, and to calibrate q. Estimates of Z_g were scaled monthly, converted to finite rates (i.e., $1 - e^{-(Z_g/12)}$), and applied to walleye ≥age-6. Walleye <age-6 were assumed to have only experienced natural mortality under the 457 mm MLL. Finite rates for younger ages were estimated from the body mass model of Peterson and Wroblewski (1984):

$$nm_{a,t,g} = \left(1 - e^{-\left(\left(1.92 \cdot {WW_{a,g}}^{-0.25}\right)/12\right)}\right) for\ a < 6$$

Female age-1 recruits was back-calculated iteratively such that predicted abundance of adult females ≥457 mm TL-at-age in November summed to $N_{FWIN,Pueblo,female}$. Proportions-at-age ≥457 mm TL were estimated from the female age-length-key. Assuming a 50:50 sex ratio of stocked fry, male age-1 recruits = female age-1 recruits. S_{fry} was computed by dividing total age-1 recruits by the mean number of fry stocked over 2003-2017 (N_{fry}; Table 1). Fry stockings were stable over this period (11.32-14.23 million annually) and represented cohorts encountered during 2018 spring egg collections and FWIN.

Boat fishing effort estimated from the 2021 creel survey incorporated non-walleye anglers and excluded months outside April─October. Total survey effort was adjusted to reflect "effective walleye effort" and increased proportionately using $P_{t\{i\}}^{boats}$ to account for fishing boat presence outside April─October for inclusion as E in the model. Catch rates were computed for each completed boat-angler trip in which at least one walleye was captured and monthly means were averaged (controlled for differences in sample size across months). Total walleye catch estimated from the 2021 creel survey was divided by the mean monthly catch rate to derive effective effort. After back-calculating recruitment and adjusting E, q was calibrated iteratively such that predicted catches over April─October summed to total creel catch (Table 1).

Fishing mortality was removed from total mortality for walleye ≥age-6 to derive the mortality schedule for simulating alternative harvest regulations. Similar to Z_g, M_g were scaled monthly and converted to finite rates. Direct estimates of M_g aligned with body mass-dependent expectations from Peterson and Wroblewski (1984) supporting application to younger ages. M_g for older ages subsumed post-release mortality. The empirical model of Reeves and Bruesewitz (2007) predicted low post-release mortality probabilities for Pueblo Reservoir and were not modeled explicitly.

The model was constructed in Microsoft Excel (version 2016). The 'Table' function was used to generate model outputs across a 3-fold range of E and q. An alternative growth scenario was examined in which female TL_{∞} and σ were reduced by 50% of the difference from male values, reflecting a lower and less variable female growth pattern when compared to baseline simulations. Low and high S_{fry} scenarios were also examined, reflecting the low and high 95% CIs derived for this parameter (Table 1). Lastly, catch-bias against males was removed by applying the female size-dependent selectivity curve to both sexes in the final scenario. Alternative scenarios were simulated at estimated/calibrated values of E and q and the standard BL = 5.

3 | RESULTS & DISCUSSION

3.1 | Population and Angler Demographics

Female walleye achieved a 39.0% longer maximum TL on average when compared to males. Variation around mean TL-at-age (denoted by σ_g) was also 39.4% higher for females (Table 1). Mean TL-at-age started to deviate between sexes at age-3 (Figure 1A). TL-at-50% maturity was shorter for males (339 mm) than females (403 mm; Figure 1C), corresponding to ages 2-3 and 3-4, respectively. Differences in mean growth patterns and variation in TL-at-age generated differences in $lp_{a,t,g}$. Under each MLL examined, $lp_{a,t,female}$ were higher than $lp_{a,t,male}$ across ages. Differences were greater under longer MLLs. Conversely, $lp_{a,t,male}$ remained elevated and exhibited an asymptotic pattern with age while $lp_{a,t,female}$ achieved a lower peak value relative to males and declined with age under each HSL. For each sex, $lp_{a,t,g}$ were higher across ages under the wide versus narrow HSL (Figure 2).

FWIN resulted in a $CPUE_{FWIN,Pueblo}$ = 1.83 fish/gang (variance = 0.15) and a $D_{FWIN,Pueblo}$ = 8.99 fish/ha (95% CI = 6.13—13.73) after applying $q_{FWIN,CCreek}$ and corresponding 95% CI. Adjusting for reservoir SA, $N_{FWIN,Pueblo}$ = 13,958 fish (95% CI = 9508—21,305), and $N_{FWIN,Pueblo,female}$ = 12,563 fish (95% CI = 8540—19,134) after adjusting for proportion female in 2018 spring egg collection catches. Estimates of annual Z_{female} from individual catch-curve regressions ranged from 0.387—0.477 (SEs = 0.092—0.167) and 0.467—0.577 (0.104—0.135) for Z_{male}. Walleye harvest from the 2021 creel survey = 2580 fish (SE = 207) and μ = 0.156 (95% CI = 0.108—0.213). Combining annual $\bar{Z}_g$ and μ resulted in $\bar{M}_{female}$ = 0.240 (finite rate = 0.213) and $\bar{M}_{male}$ = 0.327 (0.280). Linking total female mortality to $N_{FWIN,Pueblo,female}$ resulted in 45,458 (95% CI = 30,967—69,384) age-1 recruits (sexes combined) and S_{fry} = 0.00361 (95% CI = 0.00246—0.00551; Table 1).

The majority of fishing boat presence (90.0%) occurred during the standard April—October creel period and $P_{t\{i\}}^{boats}$ was greatest in June (0.204; Figure 1D). $V_{t\{i\}}^{cr}$ also consistently peaked in June across creel survey years (Figure 1E). The distribution of catch rates (fish/angler-day) computed from effective walleye boat anglers was highly variable and right-skewed. Most catch rates were ≤5 fish/angler-day (73.8% of contacts). The overall average, mean monthly catch rate was = 4.26 fish/angler-day, and the median = 1.85 fish/angler-day. Given the distribution of catch rates, only a BL = 2 was considered in addition to the standard BL = 5 in model simulations (see below). Considering effective walleye anglers only, E = 8757 angler-days (SE = 422). Total estimated walleye catches from boat anglers over April—October from the 2021 creel survey =

33,691 fish (SE = 2092). Total catch and E resulted in a calibrated $q = 0.000187$ (95% CI = 0.000123—0.000275; Table 1).

3.2 | Baseline Model Simulations

Equilibrium *SP*, adult walleye density, numbers of mature fish, and adult natural mortalities declined, while annual walleye catches and harvests increased, with increasing E and q, but non-linearly at different rates depending on the regulation examined (Figure 3 and 4). The 457 mm MLL was most protective, resulting in relatively high *SP*, adult density, and numbers of mature fish across E and q and *BLs* examined. The 305 mm and 381 mm MLLs were least protective. For example, at estimated/calibrated values of E and q and a *BL* = 5, *SP* was 65.1% and 47.0% lower under the 305 mm and 381 mm MLL compared to the 457 mm MLL, respectively (Table 2). A *BL* = 2 offset declines in *SP* at shorter MLLs to some degree, particularly under lower E and q values (Figure 3A and 4A). Overall, reducing the *BL* from 5 to 2 fish compressed the range of differences in model outputs among regulations. A *BL* = 2 was also more protective against increases in angler catch efficiency than E, since q directly influenced $CPUE_{legal,t}$ and $rp_{a,t}$ within the model. A *BL* = 2 only provided additional protections under relatively low E values where equilibrium walleye densities remained high enough for an average effective angler to achieve a daily catch rate exceeding 2 fish (Figure 3 and 4). Yet, the latter typically only occurred in May and June when walleye were most vulnerable to angler capture (Figure 1E). A *BL* (independent of size) did little to influence harvest potential during other months.

Although the model demonstrated the effectiveness of a 457 mm MLL for protecting wild broodstock, tradeoffs with recreational fishery performance measured by direct or foregone harvest potential were apparent. Although walleye catches remained highest across E and q (benefiting catch-and-release anglers; Figures 3E,F and 4E,F), harvest potential was lowest (unfavorable to harvest-oriented anglers), concentrated on females (Figure 3G and 4G) relative to males (Figure 3H and 4H), and adult natural mortalities were highest, particularly for males (Figures 3I,J and 4I,J). For example, at estimated/calibrated values of E and q and a *BL* = 5, female harvest was 50.7% higher than males, while adult male natural mortalities were 28.4% higher than females (Table 2). These patterns demonstrated foregone male harvest opportunity driven by their reduced maximum growth potential ($TL_{\infty,male}$ and σ_{male}) and $l_{pa,t,male}$ relative to females. Maximum $lp_{a,t,male}$ values under a 457 mm MLL were only ~0.40 (Figure 2B), indicating that the majority of males die from natural causes (or post-release mortality not modeled explicitly) prior to reaching legal size.

Compared to the 457 mm MLL, modeled HSLs helped balance tradeoffs between wild broodstock protection and harvest potential, resulting in intermediate population densities between the 457 mm MLL and the shorter MLLs (Figure 3B and 4B). However, the relative degree of protection differed between the narrow 381-457 mm versus wide 381-508 mm HSL. Under the narrow HSL at estimated/calibrated values of E and q and a *BL* = 5, total harvest potential increased by 55.4% and was more evenly proportioned between males (53.8%) and females (46.2%). Female harvest potential only increased by 7.1%, reflecting declining $lp_{a,t,female}$ with age as females grew beyond the upper limit of the narrow HSL and became nearly fully protected from harvest (Figure 2A). Dynamics resulted in only a 2.0% increase in mature females, but a 28.2% greater *SP* (Table 2). Although the equilibrium number of mature females was similar between regulations, survival benefits from protecting older females under the narrow HSL resulted in a greater population frequency of large-bodied, highly fecund fish, which contributed to the disproportionate increase in *SP* (Figure 5A). Broadening the HSL to 381-508 mm negated potential benefits to *SP* observed under the narrow HSL, which declined by 36.3% (Figure 3A and 4A). Female harvest increased by 27.2% under the wide HSL, reflecting elevated $lp_{a,t,female}$ across ages (Figure 2A), and contributing to reduced *SP*.

Forgone adult male harvest potential was reduced under the narrow HSL relative to the 457 mm MLL, benefiting harvest-oriented anglers. The composition of adult male mortality shifted to being predominated by harvest (54.2%) rather than natural deaths (45.8%), which diminished by 41.0% at estimated/calibrated values of E and q and a $BL = 5$. However, the number of mature males also diminished by 28.0% (Table 2), and the population size-structure of males was more truncated under the narrow HSL (Figure 5B), which could have implications for male catch during spring egg collections. Broadening the HSL to 381-508 mm had minimal influence on male dynamics relative to females (Figure 3 and 4).

3.3 | Alternative Scenarios

Reducing $TL_{\infty,female}$ and σ_{female} (each by 14.1%) had notable effects on female walleye dynamics. Importantly, *SP* and the number of mature females consistently declined by 55.3—75.5% and 41.5—60.1%, respectively, depending on the regulation relative to baseline simulations at estimated/calibrated values of E and q and a $BL = 5$ (Table 2). Values of $lp_{a,t,female}$ under the narrow and wide HSL increased across ages. As a result, *SP* under the narrow HSL was 29.8% lower than *SP* under the 457 mm MLL, which countered outcomes from the baseline growth scenario (Table 2). Other interactive processes also contributed to these outcomes. Numbers of mature females-at-age were reduced as size-dependent maturation remained constant. Lower TLs-at-age reduced WW-at-age, which increased natural mortality rates following the model of Peterson and Wroblewski (1984). Collectively however, results indicate that compressing the degree of sexual-dimorphism in body size may reduce the potential utility of a HSL in the context of wild broodstock management if relatively high proportions of females do not outgrow the upper designated limit, and/or other non-linear processes limit maturation or survival of females. The low (68.2% of baseline) and high (152.7%) S_{fry} scenarios resulted in direct proportional decreases or increases in all model outputs across regulations, except under high S_{fry} and the 305 mm MLL. In this scenario, $CPUE_{legal,t}$ was sufficient to modify $rp_{a,t}$ resulting in more dynamic responses in model outputs (Table 2). Lastly, removing catch-bias against males had a minimal influence on their dynamics (Table 2).

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TABLES

TABLE 1 | Demographic/model parameters and inputs and estimated values with standard errors (SE) or 95% confidence intervals (CI) where applicable.

Parameter	**Value**	**SE or 95% CI**
$TL_{\infty,female}$	722.518	19.301
K_{female}	0.180	0.012
$a_{0,female}$	-1.192	0.122
σ_{female}	0.102	NA
$TL_{\infty,male}$	455.258	2.547
K_{male}	0.549	0.021
$a_{0,male}$	-0.210	0.056
σ_{male}	0.086	NA
$log(A_{small})$	-12.211	0.070
B_{small}	3.106	0.012
$c_{WW,small}$	1.007	NA
$log(A_{large})$	-14.433	2.150
B_{large}	3.470	0.331
$c_{WW,large}$	1.008	NA
$\beta_{0,female}$	-22.169	1.811
$\beta_{1,female}$	0.055	0.004
$\beta_{0,male}$	-16.895	1.247
$\beta_{1,male}$	0.050	0.003
α	0.00000129	NA
β	3.947	NA
$\bar{Z}_{female}$	0.432	0.019
$\bar{S}_{female}$	0.649	0.013
$\bar{S}_{male}$	0.530	0.025
$\bar{S}_{male}$	0.589	0.015
a_{max}	15	NA
$TL_{1,female}$	408.937	4.802
$TL_{2,female}$	560.406	25.789
$k_{1,female}$	45.745	5.480
$k_{2,female}$	133.999	21.694
φ_{female}	0.541	0.054
$TL_{1,male}$	409.786	3.803
$TL_{2,male}$	568.103	32.227
$k_{1,male}$	48.440	4.287
$k_{2,male}$	122.063	23.301
φ_{male}	0.308	0.041
N_{fry}	12,599,187	246,759
S_{fry}	0.00361	0.00246—0.00551*
N_1	45,458	30,967—69,384*
μ	0.156	0.108—0.213*
E	8757	422
q	0.000187	0.000123—0.000275*

*Uncertainty reflects application of $q_{FWIN,CCreek}$ and associated 95% confidence interval. Uncertainty in point estimates used to derive these quantities was not considered.

TABLE 2 | Equilibrium model outputs from alternative growth and angler selectivity scenarios at estimated/calibrated values of *E* and *q* for each length-based harvest regulation examined (MLL = minimum length limit; HSL = harvest slot limit). Spawn potential is millions of eggs. Age-3+ walleye density (sexes combined) was calculated from conservation pool elevation (nmorts = natural mortalities). Values in parentheses represent ± percent changes from baseline growth.

Model output	**Baseline growth**	**Reduced female growth**	**Low S_{fry}**	**High S_{fry}**	**No catch-bias against males**
Regulation: 305 mm MLL (BL = 5)					
Spawn potential (*SP*)	218.01	65.29 (-70.1)	148.64 (-31.8)	410.60 (88.3)	218.01 (0.0)
Age-3+ density (#/ha)	11.59	12.77 (10.2)	7.90 (-31.8)	19.41 (67.5)	11.39 (-1.7)
Mature females	5745	2358 (-59.0)	3917 (-31.8)	10,139 (76.5)	5745 (0.0)
Mature males	13,568	13,568 (0.0)	9251 (-31.8)	22,124 (63.1)	13,230 (-2.5)
Female catch	8326	5669 (-31.9)	5677 (-31.8)	13,529 (62.5)	8326 (0.0)
Male catch	7489	7489 (0.0)	5106 (-31.8)	12,199 (62.9)	7994 (6.7)
Female harvest	7199	4674 (-35.1)	4909 (-31.8)	10,408 (44.6)	7199 (0.0)
Male harvest	6969	6969 (0.0)	4751 (-31.8)	10,049 (44.2)	7129 (2.3)
Female nmorts (age-3+)	2068	3061 (48.0)	1410 (-31.8)	3639 (76.0)	2068 (0.0)
Male nmorts (age-3+)	2334	2334 (0.0)	1591 (-31.8)	4050 (73.5)	2253 (-3.5)
Regulation: 381 mm MLL (BL = 5)					
Spawn potential (*SP*)	330.48	118.67 (-64.1)	225.32 (-31.8)	504.68 (52.7)	330.48 (0.0)
Age-3+ density (#/ha)	16.08	16.97 (5.5)	10.96 (-31.8)	24.56 (52.7)	16.05 (-0.2)
Mature females	8239	3992 (-51.5)	5618 (-31.8)	12,582 (52.7)	8239 (0.0)
Mature males	17,830	17,830 (0.0)	12,157 (-31.8)	27,229 (52.7)	17,780 (-0.3)
Female catch	10,473	7618 (-27.3)	7141 (-31.8)	15,994 (52.7)	10,473 (0.0)
Male catch	10,032	10,032 (0.0)	6840 (-31.8)	15,320 (52.7)	10,735 (7.0)
Female harvest	5772	3421 (-40.7)	3936 (-31.8)	8815 (52.7)	5772 (0.0)
Male harvest	5065	5065 (0.0)	3453 (-31.8)	7735 (52.7)	5088 (0.5)
Female nmorts (age-3+)	3009	4247 (41.1)	2052 (-31.8)	4596 (52.7)	3009 (0.0)
Male nmorts (age-3+)	3673	3673 (0.0)	2504 (-31.8)	5609 (52.7)	3660 (-0.4)
Regulation: 457 mm MLL (BL = 5)					
Spawn potential (*SP*)	623.96	278.93 (-55.3)	425.42 (-31.8)	952.87 (52.7)	623.96 (0.0)
Age-3+ density (#/ha)	23.79	24.10 (1.3)	16.22 (-31.8)	36.33 (52.7)	23.79 (0.0)
Mature females	13,394	7831 (-41.5)	9132 (-31.8)	20,455 (52.7)	13,394 (0.0)
Mature males	25,986	25,986 (0.0)	17,717 (-31.8)	39,684 (52.7)	25,985 (0.0)
Female catch	13,668	10,598 (-22.5)	9319 (-31.8)	20,873 (52.7)	13,668 (0.0)
Male catch	15,026	15,026 (0.0)	10,245 (-31.8)	22,947 (52.7)	15,763 (4.9)
Female harvest	3795	1875 (-50.6)	2588 (-31.8)	5796 (52.7)	3795 (0.0)
Male harvest	1872	1872 (0.0)	1276 (-31.8)	2859 (52.7)	1872 (0.0)
Female nmorts (age-3+)	4854	5786 (19.2)	3310 (-31.8)	7413 (52.7)	4854 (0.0)
Male nmorts (age-3+)	6778	6778 (0.0)	4622 (-31.8)	10,352 (52.7)	6778 (0.0)
Regulation: 381-457 mm HSL (BL = 5)					
Spawn potential (*SP*)	800.06	195.78 (-75.5)	545.49 (-31.8)	1221.81 (52.7)	800.06 (0.0)
Age-3+ density (#/ha)	19.61	18.30 (-6.7)	13.37 (-31.8)	29.95 (52.7)	19.58 (-0.2)
Mature females	13,658	5448 (-60.1)	9312 (-31.8)	20,858 (52.7)	13,658 (0.0)
Mature males	18,708	18,708 (0.0)	12,755 (-31.8)	28,570 (52.7)	18,655 (-0.3)
Female catch	12,855	8432 (-34.4)	8765 (-31.8)	19,632 (52.7)	12,855 (0.0)

Male catch	10,562	10,562 (0.0)	7202 (-31.8)	16,130 (52.7)	11,264 (6.6)
Female harvest	4064	2959 (-27.2)	2771 (-31.8)	6207 (52.7)	4064 (0.0)
Male harvest	4734	4734 (0.0)	3228 (-31.8)	7230 (52.7)	4758 (0.5)
Female nmorts (age-3+)	4579	4669 (2.0)	3122 (-31.8)	6993 (52.7)	4579 (0.0)
Male nmorts (age-3+)	4001	4001 (0.0)	2728	6110	4001
Regulation: 381-508 mm HSL (BL = 5)					
Spawn potential (*SP*)	509.90	133.36 (-73.8)	347.65 (-31.8)	778.69 (52.7)	509.90 (0.0)
Age-3+ density (#/ha)	17.21	17.16 (-0.3)	11.74 (-31.8)	26.29 (52.7)	17.18 (-0.2)
Mature females	10,202	4263 (-58.2)	6856 (-31.8)	15,580 (52.7)	10,202 (0.0)
Mature males	17,895	17,895 (0.0)	12,201 (-31.8)	27,329 (52.7)	17,845 (-0.3)
Female catch	11,287	7763 (-31.2)	7695 (-31.8)	17,236 (52.7)	11,287 (0.0)
Male catch	10,072	10,072 (0.0)	6867 (-31.8)	15,381 (52.7)	10,775 (7.0)
Female harvest	5171	3340 (-35.4)	3525 (-31.8)	7897 (52.7)	5171 (0.0)
Male harvest	5041	5041 (0.0)	3437 (-31.8)	7698 (52.7)	5064 (0.5)
Female nmorts (age-3+)	3557	4321 (21.5)	2425 (-31.8)	5432 (52.7)	3557 (0.0)
Male nmorts (age-3+)	3697	3697 (0.0)	2521 (-31.8)	5646 (52.7)	3684 (-0.4)

FIGURES

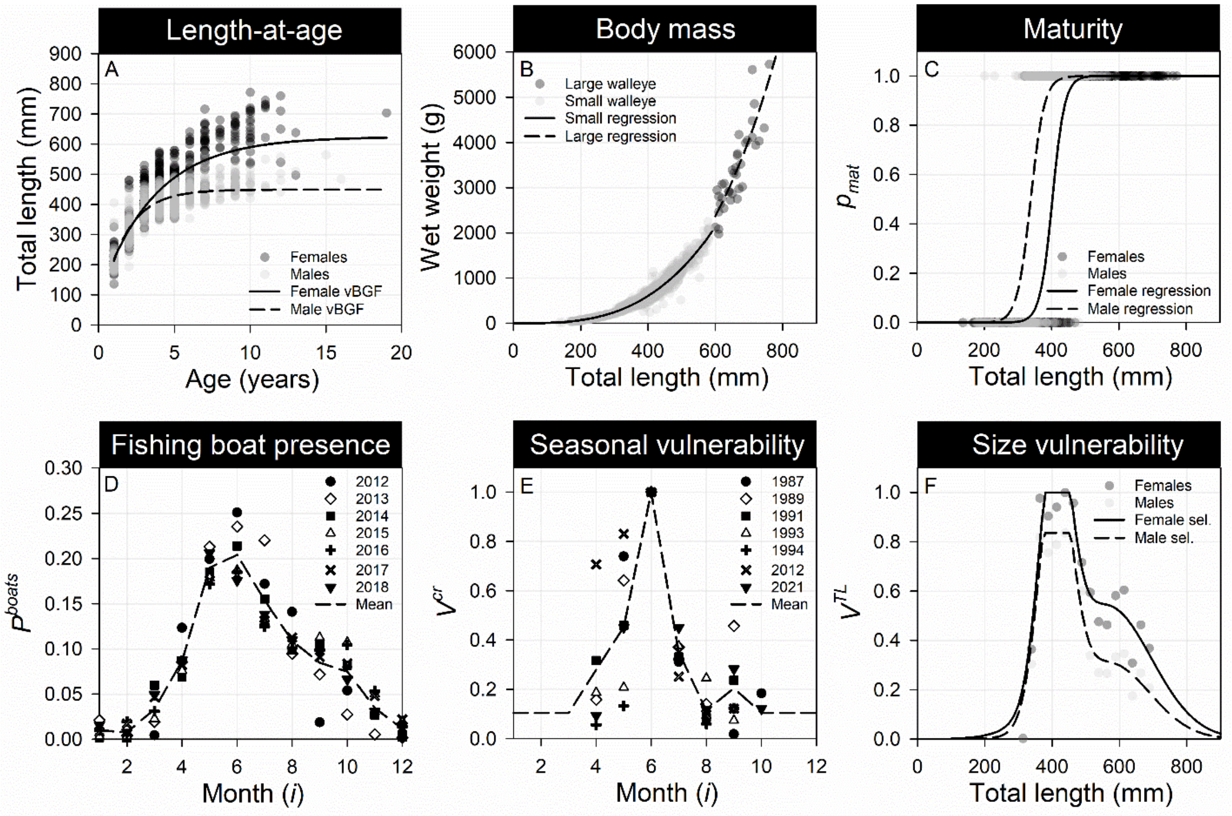

FIGURE 1 | Top row: walleye demographics including sex-dependent length-at-age (A; lines = fitted vBGFs), body mass versus total length for small and large fish (B; lines = fitted regressions), and length-dependent maturity by sex (C; lines = fitted logistic regression models). Bottom row: angler dynamics including proportional fishing boat presence (P^{boats}; D; dashed line connects means by month), seasonal vulnerability of walleye to angler capture (V^{cr}; E; dashed line connects means by month), and sex-dependent size-selectivity of anglers for walleye (V^{TL}; F; lines = fitted join gaussian functions). The abbreviation vBGF = von Bertalanffy Growth Function, and sel. = selectivity.

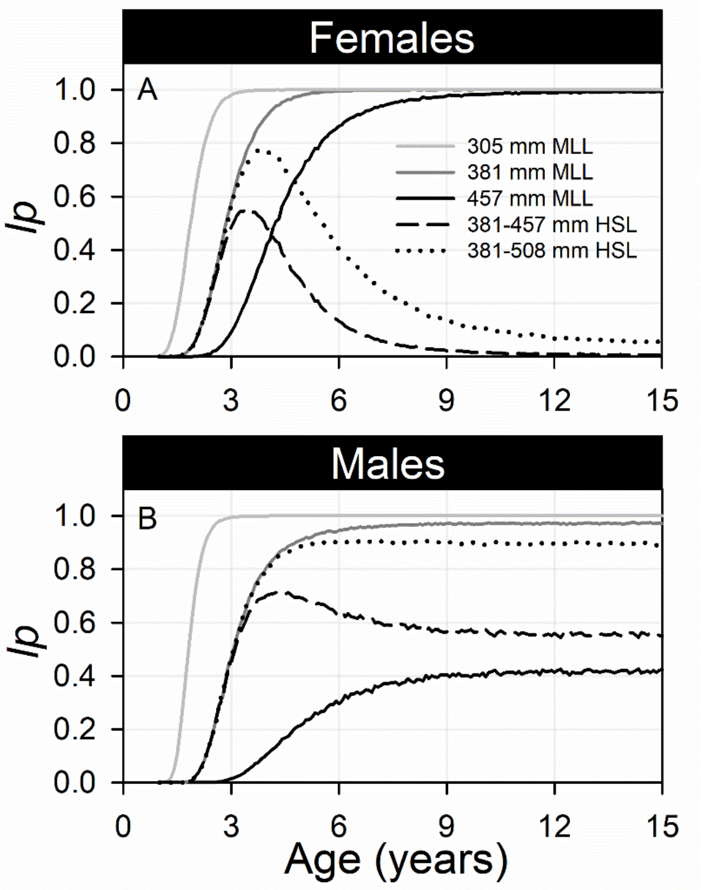

FIGURE 2 | Age-specific probabilities of being legal size (*lp*) for female (A) and male (B) walleye under five length-based harvest regulations (MLL = minimum length limit; HSL = harvest slot limit).

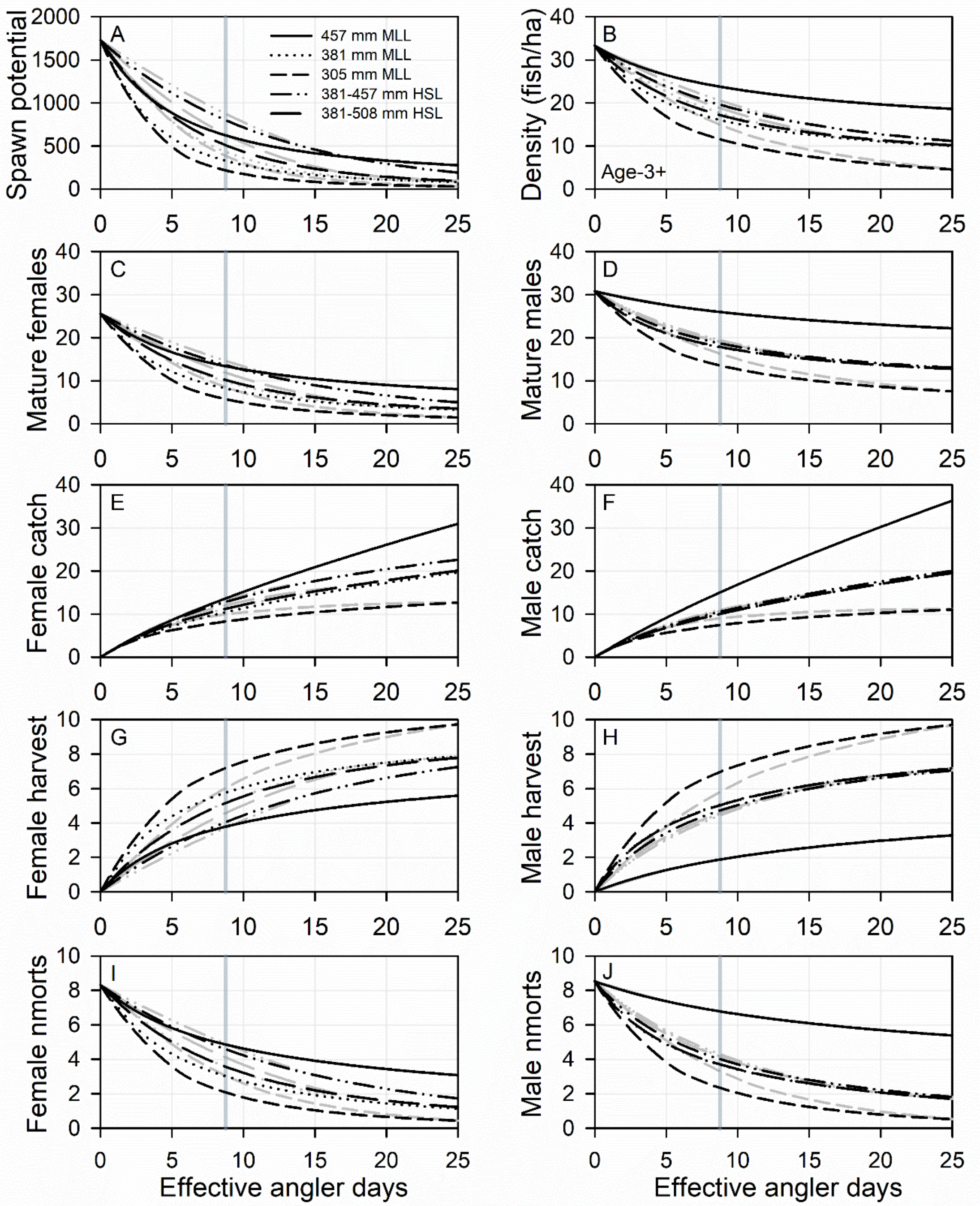

FIGURE 3 | Equilibrium model outputs versus annual fishing effort (1000s of effective angler-days) for each length-based harvest regulation examined with a daily *BL* of 5 (black lines) versus 2 (gray lines) walleye. Units for spawn potential (A) are in millions of eggs. Walleye density estimates (B) are for adults ≥age-3 (sexes combined) at conservation pool elevation. Units for the number of mature walleye by sex (C and D), catch by sex (E and F), harvest by sex (G and H), and natural mortalities (nmorts; age-3+) by sex (I and J) are in 1000s. The vertical reference line = effective effort estimated during the 2021 creel survey (8757 angler-days).

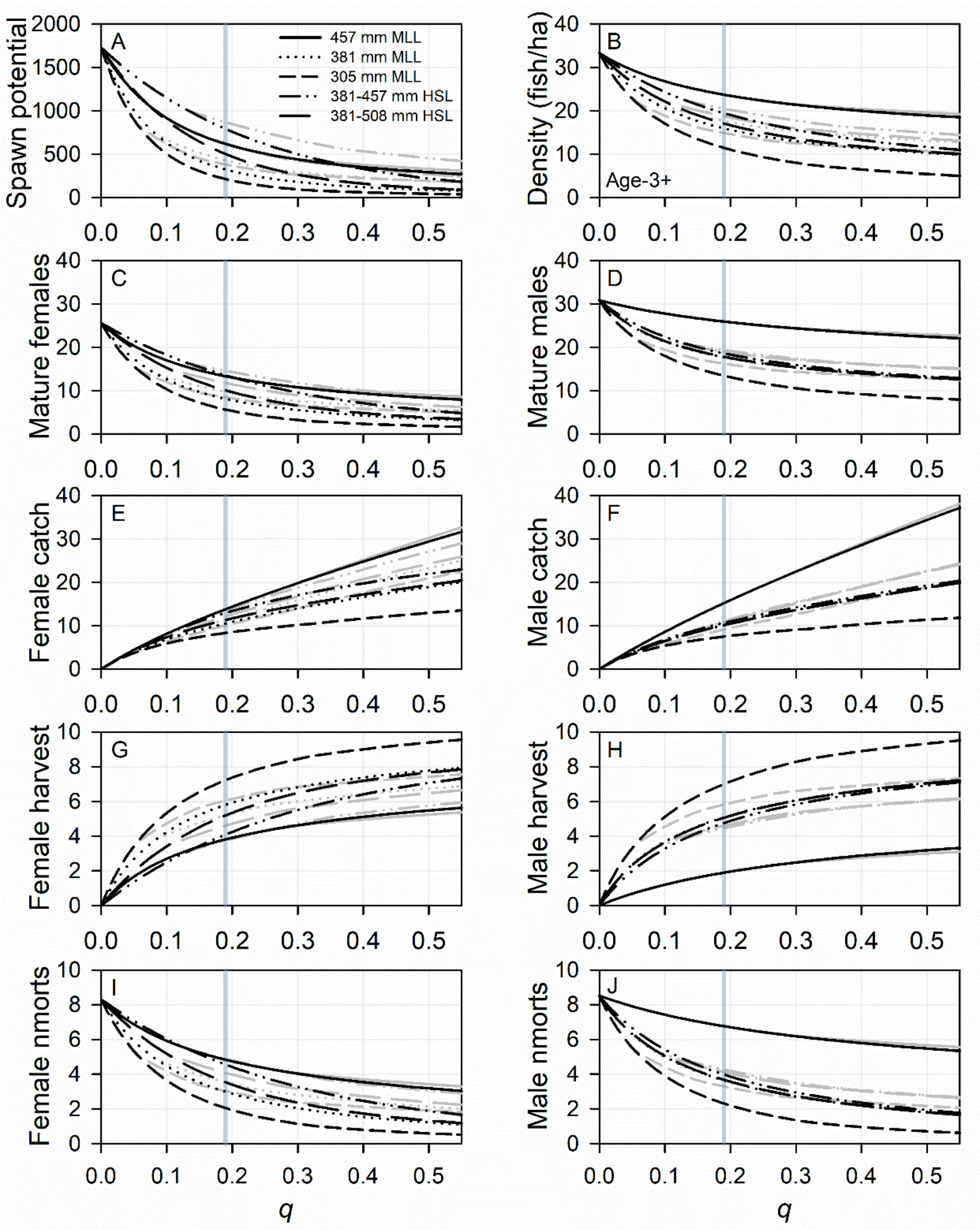

FIGURE 4 | Equilibrium model outputs versus fully-selected angler catch efficiency (*q*; angler·day^{-1} scaled by a factor of 1000 for plotting) for each length-based harvest regulation examined with a daily *BL* of 5 (black lines) versus 2 (gray lines) walleye. Units for spawn potential (A) are in millions of eggs. Walleye density estimates (B) are for adults ≥age-3 (sexes combined) at conservation pool elevation. Units for the number of mature walleye by sex (C and D), catch by sex (E and F), harvest by sex (G and H), and natural mortalities (nmorts; age3+) by sex (I and J) are in 1000s. The vertical reference line = calibrated *q* value (0.000187 angler·day^{-1} scaled by a factor of 1000).

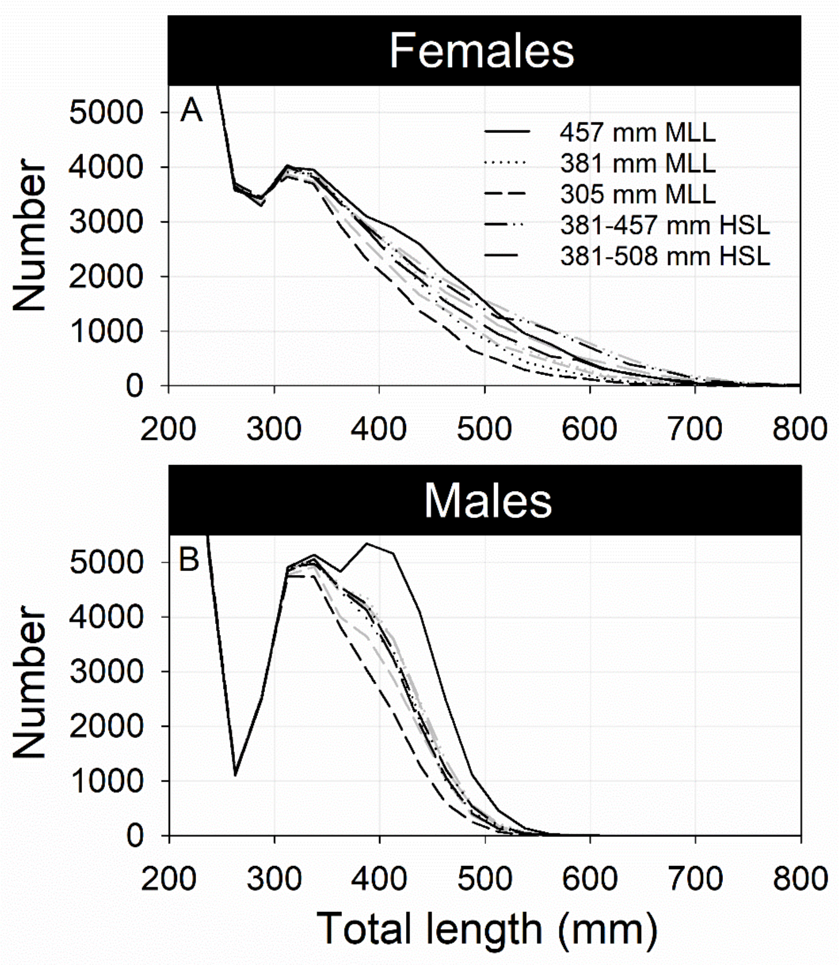

FIGURE 5 | Simulated equilibrium size-structure for female (A) and male (B) walleye under five length-based harvest regulations and a daily *BL* of 5 (black lines) versus 2 (gray lines) fish (MLL = minimum length limit; HSL = harvest slot limit). Size-structures were simulated from parameters of the vBGFs using equilibrium numbers-at-age present in March at the estimated/calibrated values of *E* and *q*.

RESEARCH PRIORITY: **Walleye oxytetracycline marking:** Exploring the potential of mass marking Walleye with oxytetracycline.

OBJECTIVES

The primary objective of this priority is to determine if oxytetracycline (OTC) can be used effectively to mark Walleye at multiple life stages.

BACKGROUND

Marking fish (individually or in groups) is a crucial component for answering many questions related to fisheries. For example, batch marking and recapturing fish can help determine the prevalence of natural reproduction, population size and population growth. Marking fish with individual identifiers can help determine individual growth, movement, survival and other demographic characteristics at the individual and population level. Initially, investigation was focused on fish marking techniques to aid in the assessment of Walleye fry versus fingerling success after stocking, wiper *Morone saxatilis* x *M. chrysops* stocking success, and balancing Walleye and wiper stocking in systems to support sympatric populations. Early efforts reduced marking options and selected oxytetracycline (OTC) emersion marking over other approaches using calcein and alizarin red for a variety of reasons including disposal and regulation (Lepak 2013).

PROJECT PROGRESS

In 2025, Walleye fry and fingerling stocked into Jumbo Annex were marked with OTC. Walleye fry (~200,000) were marked in transit from the Wray Hatchery to Jumbo Annex on April 8th (right). Additionally, Walleye fry (~160,000) were marked with OTC at the Pueblo Hatchery and moved into a holding pond on April 25th. On June 10th, 4,000 of these fish (survival was nearly 50% for these OTC marked Walleye) were collected as fingerlings and marked with OTC again while in transit for stocking into Jumbo Annex. Age-0 Walleye from stocking or natural reproduction in 2025 were collected in October by Mandi Brandt and will be processed to determine if OTC marking was successful, and if we can differentiate between the relative success/survival/growth of Walleye reproduced naturally (no OTC mark), Walleye stocked as fry (one OTC mark), and Walleye stocked as fingerlings (two OTC marks).

The OTC marking described above was conducted similarly to past efforts. An OTC marking protocol developed by Brooks et al. (1994) and refined by the Minnesota Department of Natural Resources (see Logsdon et al. 2004) was used to mark Walleye fry and fingerlings. Briefly, this method involves adding OTC (Pennox® 343 soluble powder; 76% OTC) to the treatment water at 700 mg/L and then bringing the pH of the solution up to approximately 6.8 using an appropriate amount of sodium phosphate, dibasic, anhydrous buffer depending on the water alkalinity. Fish are then placed in the solution for six hours and removed after this treatment. However, we were also interested in the effectiveness of using an emersion time less than six hours. The emersion can be stressful on fish, and limiting the time in the OTC solution could improve survival during marking. Thus, we marked a small number of fingerling Walleye using emersion times of three and five hours to determine if the shorter time period would still produce visible OTC marks in Walleye. We also tested a small number of Walleye fingerlings using OTC that was older than our recently purchased Pennox® 343 to determine if older OTC would still mark Walleye effectively. Finally, we used water from the Wray hatchery to mark a small number of Walleye fingerlings to validate that water could be used successfully (appropriate chemical makeup) to mark Walleye at that facility. These smaller groups of Walleye were held in tanks for ~3 weeks to promote otolith growth beyond any OTC marks to facilitate detection. These Walleye and those collected from Jumbo Annex will be processed and analyzed in 2026 to determine the success of these efforts.

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Lepak, J. M. 2013. Annual lake and reservoir research report. Colorado Parks and Wildlife. Annual Report, Fort Collins, CO, USA.

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RESEARCH COMMUNICATION & TECHNICAL ASSISTANCE

Reporting period: December 2024 – November 2025.

Peer-Reviewed Publications

- Farrell, C. J., B. M. Johnson, **A. G. Hansen, B. W. Avila,** and C. M. Myrick. 2025. Induced sterility illuminates the effects of reproduction on growth. Canadian Journal of Fisheries and Aquatic Sciences 82:1-13.

- **Lepak, J. M., A. G. Hansen,** B. M. Johnson, K. Battige, E. T. Cristan, C. J. Farrell, W. M. Pate, **K. B. Rogers, A. J. Treble,** and T. E. Walsworth. 2025. Cyclical, multi-trophic-level responses to a volatile, introduced forage fish: learning from four decades of food web observation to inform management. Fisheries 50:52-65.

- **Lepak, J. M., A. G. Hansen,** T. L. Martinez, E. A. Stewart, D. J. Pinkus, A. M. Pelletier, and **A. J. Treble.** 2025. Maximum age of Bighead Carp *Hypophthalmichthys nobilis* exceeds 30 years: implications for anticipating invasive species establishment and impacts. Journal of Fish Biology 2025:1-8. DOI: 10.1111/jfb.70181.

- Walsworth, T. E., **A. G. Hansen,** and **J. M. Lepak.** 2025. Alternating ecosystem states driven by an invasive fish in a life history intraguild predation system. Canadian Journal of Fisheries and Aquatic Sciences 82:1-15.

- **Hansen, A. G., J. M. Lepak,** W. M. Pate, D. Brauch, and **B. W. Avila.** 2025. Just water over the dam? Reservoir fishery disruption following drought-mediated reoperation for environmental flows. Ecosphere 16(10):1-19.

Technical Publications

- **Lepak, J. M., A. G. Hansen,** A. J. Treble, and E. A. Stewart. 2025. Gizzard Shad (*Dorosoma cepedianum*) in Colorado lakes, reservoirs and ponds: background, generalizations, system-specific examples, control, and alternatives. Technical Publication No. 67, CPW-R-T-67-25, ISSN 0084-8883. Colorado Parks and Wildlife, Aquatic Research Section, Fort Collins, Colorado.

Manuscripts in Preparation

- **Hansen, A. G.,** C. Tucker, and **J. M. Lepak.** Exploiting sexually dimorphic growth to improve wild broodstock management of a popular sport fish. In preparation for Fisheries Management and Ecology.

- **Lepak, J. M., A. G. Hansen,** T. Klee, T. L. Martinez, and T. E. Walsworth. The role of predation versus cannibalism in an ecosystem driven by reciprocal life-history intraguild predation dynamics. In preparation for Canadian Journal of Fisheries and Sciences.

External Presentations

- **Firestone, T. B. R.,** C. Baum, K. Morben, R. Dils, B. Avila, and **J. M. Lepak.** 2025. From fish collection to data analysis. Continuing education class held at the American Fisheries Society Western Division Meeting. Westminster, Colorado. May 2025.

- **Hansen, A. G., J. M. Lepak,** W. M. Pate, D. Brauch, and **B. W. Avila.** 2025. Just water over the dam? Reservoir fishery disruption following reoperation for environmental flows. Western Division of the American Fisheries Society. Westminster, Colorado. May 2025.

- **Lepak, J. M.** 2025. Characterizing lake and reservoir food webs: simple and complex models. Guest lecture for Front Range Community College. Fort Collins, Colorado. April 2025.

- **Lepak, J. M.** 2025. Sterile tiger muskellunge (*Esox lucius* x *E. masquinongy*) as undesirable fish species control agents. Poster presentation. Western Division American Fisheries Society Meeting. Westminster, Colorado. May 2025.

- **Lepak, J. M., A. G. Hansen,** B. M. Johnson, K. Battige, E. T. Cristan, C. J. Farrell, W. M. Pate, **K. B. Rogers, A. J. Treble,** T. E. Walsworth, and M. Sandersen. 2025. Cyclic, multi-trophic-level responses to a volatile, introduced forage fish: Learning from four decades of food web observation to inform management. Western Division American Fisheries Society Meeting. Westminster, Colorado. May 2025.

Internal Presentations

- **Hansen, A. G., J. M. Lepak,** W. M. Pate, D. Brauch, and **B. W. Avila.** 2025. Did dam reoperation facilitate lake trout expansion in Blue Mesa Reservoir, Colorado? Colorado Parks and Wildlife Coldwater Reservoir Management Meeting. Buena Vista, Colorado. January 2025.

- **Lepak, J. M.** 2025. Tiger muskellunge update, College Lake comparison, Grand Lake mesocosms. Colorado Parks and Wildlife Coldwater Reservoir Meeting. Buena Vista, CO. January 2025.

- **Lepak, J. M., A. G. Hansen,** and **A. J. Treble.** 2025. Colorado Parks and Wildlife fisheries data entry and standardization. Aquatic Section Meeting Biologist Summit. Mount Princeton, CO. February 2025.

Other Research Communication & Technical Assistance

- Peer reviewer for: Canadian Journal of Fisheries and Aquatic Sciences (2), Ecosystems (1), Fisheries Research (2), Michigan Sea Grant (1), North American Journal of Fisheries Management (2), Transactions of the American Fisheries Society (1).

- Consultations with Jon Ewert (Shadow Mountain Reservoir), Alex Townsend (Clear Creek Reservoir), Kira Paik (Spinney Reservoir, Northern Pike cleithra), Mark Sandersen (Joe Wright

Reservoir, Big Creek Reservoir, Seaman Reservoir), Gage Dean (Elkhead Reservoir), Ben Swigle (Largemouth Bass management), Jim White (Navajo Reservoir), and Eric Gardunio (Ridgway Reservoir, Crawford Reservoir).

- Consultation with Quentin Springer at Pueblo Hatchery, Tyler Baker at Wray Hatchery, and Mandi Brandt regarding Walleye OTC marking.