COLDWATER LAKE AND RESERVOIR RESEARCH

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COLDWATER LAKE AND RESERVOIR RESEARCH

Period covered: December 2021 – November 2022.

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

RESEARCH PRIORITY: **Summer Profundal Index Netting for monitoring Lake Trout *Salvelinus namaycush*:** Results from 2022 sampling on Blue Mesa Reservoir.

OBJECTIVES:

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

INTRODUCTION:

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

Summer Profundal Index Netting (SPIN) is a quantitative survey method for rapidly estimating the density of Lake Trout (Sandstrom and Lester 2009). Previous investigations by Colorado Parks and Wildlife concluded that SPIN is a viable alternative to more intensive methods for estimating and tracking trends in the abundance of Lake Trout to help guide management (Lepak 2011; Lepak 2013). Four water bodies have been sampled using SPIN: Taylor Park Reservoir (surveyed in 2013), Lake Granby (2014), Grand Lake (2013, 2016), and Blue Mesa Reservoir (2011, 2014, 2016, 2018, 2020, and 2021). Results from the 2022 survey on Blue Mesa Reservoir are reported here.

METHODS:

SPIN uses suites of standardized gill nets (three 1.8 × 64 m nets consisting of eight panels with mesh sizes of 57-, 64-, 70-, 76-, 89-, 102-, 114- and 127-mm stretch measure placed in random order) to capture Lake Trout in a way that allows us to estimate 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 three days from August 2-4, 2022, wherein 79 nets were set, capturing a total of 151 Lake Trout ranging in size from 228 mm to 830 mm FL (mean = 364 mm ± 106 mm SD). Lake Trout were most prevalent in 30-40 m depths across Cebolla and Sapinero basins. No Lake Trout were encountered in Iola, likely due to the low reservoir elevations observed in 2022. The depth distribution, size structure, and extent of the catch in 2022 at the corresponding water surface elevation of the reservoir produced a total Lake Trout abundance estimate of 12,477 fish ≥228 mm FL (lower 68% confidence limit = 9,451; upper limit = 15,864). The catch of Lake Trout <250 mm FL was incidental (3.31%). Therefore, these abundance estimates best reflect those of fish ≥250 mm FL as in previous SPIN surveys on Blue Mesa Reservoir (Sandstrom and Lester 2009; Table 1).

In 2018, a reduced abundance of piscivorous-sized Lake Trout (estimated from SPIN) and a notable boost in the abundance of kokanee *Oncorhynchus nerka* (estimated from hydroacoustics) was observed. Therefore, fall suppression netting (ongoing since 2009) was not completed in 2018 or 2019. Rather, an incentivized angler harvest tournament for Lake Trout ≤660 mm TL was conducted winter through early summer in 2020 in anticipation for a pulse of small fish observed in 2018 entering the size range fully vulnerable to anglers. Thus, the 2020 SPIN survey was completed after the tournament was concluded and reflects angler harvest that accrued earlier in the year. Tournament anglers turned in 4,055 Lake Trout, 44% (1,791) of which were fish ≥400 mm TL. The smallest fish turned in was 203 mm TL. Relative to 2018, the estimated abundance of all fish vulnerable in 2020 was much reduced, whereas the estimated abundance of piscivorous-sized fish was slightly elevated, supporting the notion that small fish observed in 2018 recruited into the piscivorous size range as anticipated (Figure 1). The higher relative frequency of fish ≥400 mm observed in the SPIN catch in 2020 compared to 2018 also supported this notion (Figure 2).

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

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

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

The angler harvest incentive tournament was repeated in 2021 to reinforce results from 2020 and apply continued harvest pressure to the population of small Lake Trout. In 2021, 178 anglers participated turning in 1,704 heads, which was down from 2020 when 338 anglers participated and turned in 4,055 heads. Anglers generally captured larger fish in 2021 when compared to 2020, and the majority of heads were from fish >400 mm TL. Despite the reduced angler participation, SPIN estimates from 2021 (for all fish vulnerable and for most piscivorous fraction) were lower than those in 2020 (Figure 1), indicating that harvest levels being achieved during the tournaments (combined with natural mortality) were sufficient for keeping small Lake Trout in check. In addition, there was not a significant difference in the size-structure of Lake Trout captured during SPIN in 2021 versus 2020 ($P > 0.95$), but a highly significant difference ($P < 0.001$) between 2021 and 2018 (when a large pulse of small fish was moving through the system), suggesting that there would not be a large crop of small fish for anglers to catch in 2022 and the tournaments to date were successful. For these reasons, a tournament was not conducted prior to SPIN during 2022.

In addition to the biological reasons for not conducting a tournament in 2022, this decision also helped demonstrate to anglers the adaptive nature of the harvest incentive program and how up-to-date survey information is used to inform management decisions (an important component needed to garner angler support at the onset of program). The 2022 SPIN survey demonstrated a slight increase in the numbers of all fish vulnerable, but a continued decrease in the numbers of piscivorous-sized fish. This outcome helped corroborate our current understanding of Lake Trout population dynamics in Blue Mesa Reservoir. Based on previous research, we expected the Lake Trout population to be resilient to harvest, and therefore, expected numbers of all Lake Trout vulnerable to harvest to increase during 2022 since no tournament was conducted and small Lake Trout vulnerable to sampling should be continuously recruiting into the system. However, it also takes time for these new recruits to grow to piscivorous size, so a lag should be observed before we see those fish appear in the piscivorous size-class. Collectively, patterns continue to indicate that anglers alone, through periodic incentivized harvest, can help keep piscivorous Lake Trout numbers in Blue Mesa Reservoir at a level conducive to supporting a robust Kokanee population. However, it also suggests that such patterns are sensitive to the frequency of tournaments, and that we should consider another tournament in 2023 or 2024.

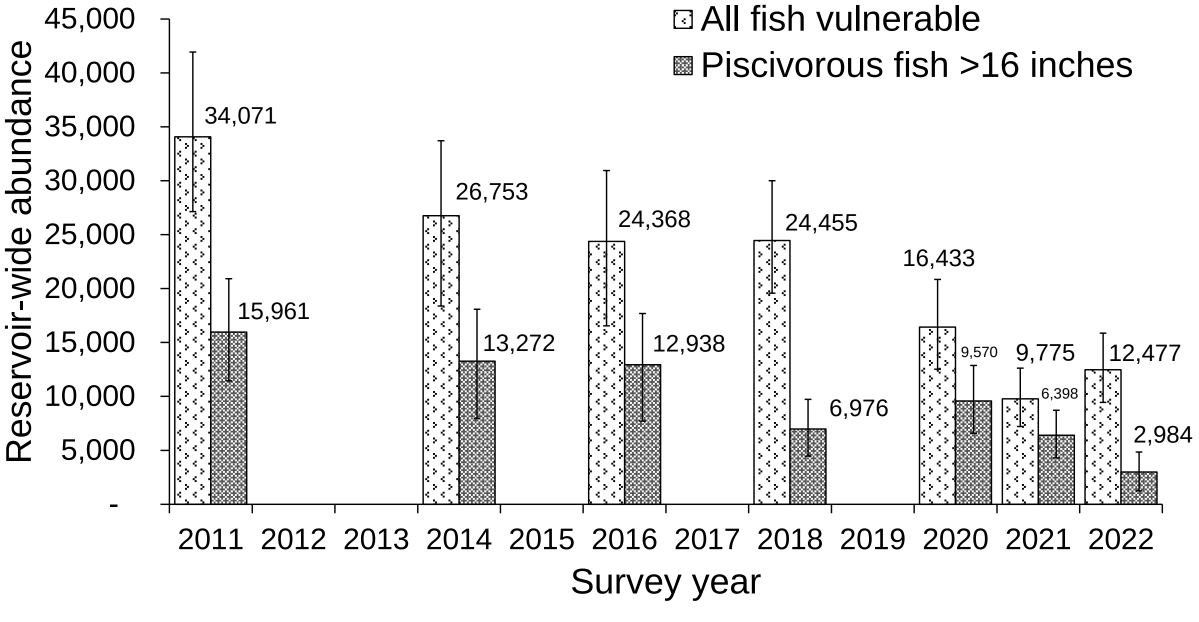

Figure 1. Abundance estimates for all Lake Trout vulnerable to the sampling gear (generally those ≥250 mm FL or 275 mm TL) in Blue Mesa Reservoir (white bars) and just those ≥363 mm FL or 400 mm TL (gray bars) from all SPIN surveys conducted to date. Error bars represent 68% confidence intervals.

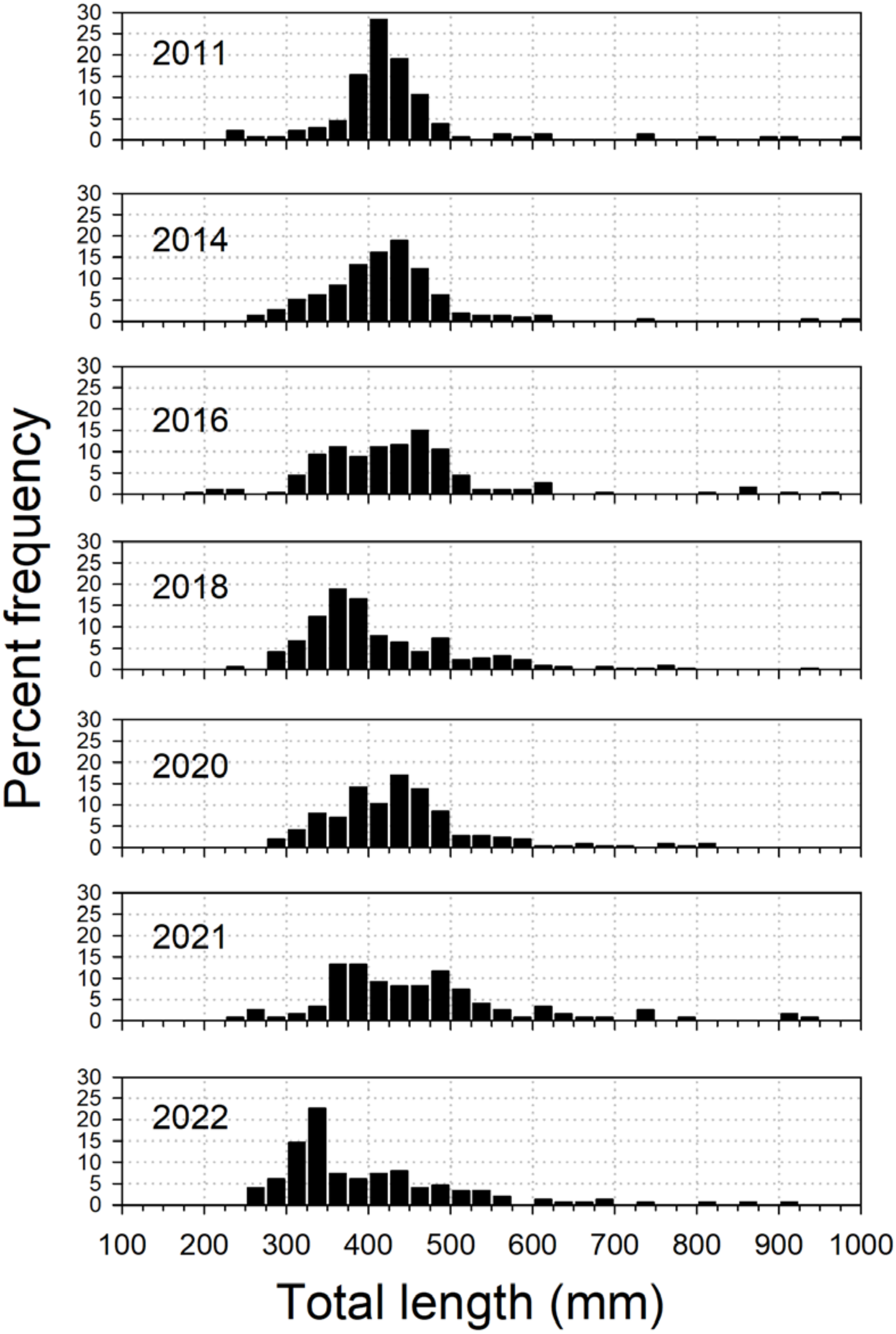

Figure 2. Length-frequency distributions (25 mm size bins) of Lake Trout captured during consecutive SPIN surveys on Blue Mesa Reservoir.

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<u>**RESEARCH PRIORITY**</u>: **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 *Micropterus dolomieu*, and White Sucker *Catostomus comersonii*), 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.

INTRODUCTION:

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 *Oncorhynchus 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 *O. mykiss*, 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 the potential to slow the spread of gill lice to native fish populations in some unique 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 *Sander vitreus*) 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

- Conceptualization and design planning for antenna arrays in three locations in Shadow Mountain Reservoir was completed in early spring 2022.

- 2 antenna array location site visits occurred to ground-truth engineering design plans of the concrete structures on which the antenna arrays are to be mounted/installed.

- A Special Use Permit (SUP) was developed to work with the Bureau of Reclamation’s work envelopes in all 3 antenna locations.

- The SUP was submitted May 19th, 2022, one month after a meeting with Jon Ewert and Bureau of Reclamation personnel discussing the permitting process.

- Although we have been in contact with BOR (Traci Robb), the application process is not complete, and we have no indication of what may or may not be approved related to our study design if/when our application does get approved.

- Project personnel are currently considering alternatives to address this permitting issue.

- CPW personnel conducted routine gill netting in Shadow Mountain Reservoir (20 experimental gill nets set for 6 hours); data have not been fully processed.

Elkhead Reservoir

- Elkhead Reservoir was stocked by CPW personnel with 2,833 Floy tagged tiger muskellunge on August 29 and 30, 2022 in a protected cove near artificial structures where Northern Pike catch rates are generally lowest during routine sampling efforts.

- A subset of 274 tiger muskellunge ranged in length from 125-197 mm with a mean of 160 mm. They ranged in weight from 10-40 g with a mean of 21 g. These fish were much smaller than anticipated (i.e., >300 mm).

- A subset (N = 100) of tagged tiger muskellunge were retained in a 1 cm stretch mesh holding pen (~ 1 m^3) overnight from 30 August to 31 August 2022 to determine short-term tagging mortality and tag loss in the holding pen environment.

- Of the 100 fish held, two were found dead in the pen the following day, but all 100 retained their Floy tags. Similarly, short term Floy tag retention and survival of other esocids (Northern Pike) tagged and stocked in this system in the past has been high (exceeding 99%; Tory Eyre personal communication).

- Routine CPW sampling and marking efforts included trap netting (Northern Pike) and night electrofishing (Smallmouth Bass) prior to an incentivized angler tournament in summer 2022 targeting both species for removal; data have not been fully processed.

Overall project components

- A Research Associate was identified and hired to focus on the project Oct. 10th, 2022.

- The Research Associate has been in contact with Shadow Mountain and Elkhead reservoir managers/biologists Jon Ewert and Tory Eyre about their management approaches.

- Project personnel have visited the University of Wyoming to observe and conduct fish eye lens extraction and dissection procedures.

- The statewide request from Colorado managers for tiger muskellunge was not met in 2022 and this shortfall meant that Shadow Mountain Reservoir was not stocked with tiger muskellunge, while Elkhead Reservoir was stocked with 2,833 small (~160 mm) tiger muskellunge versus the 1,000 large (>300 mm) fish originally expected.

- Though this alteration in stocking was unexpected, it provides the opportunity to compare the post-stocking success of different size classes of tiger muskellunge.

- Project personnel visited the CPW fish hatchery in Wray to discuss and plan potential timing and logistics for future stocking efforts to improve outcomes.

- The Research Associate has begun compiling and reviewing data available from 114 lakes and reservoirs stocked with tiger muskellunge in Colorado from 1983 to 2021 (730 individual stocking events) to search for broad scale patterns to inform management decisions related to tiger muskellunge stocking densities and timing.

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RESEARCH PRIORITY: **Informing tiger trout (Brook Trout *Salvelinus fontinalis* × Brown Trout *Salmo trutta*) stocking procedures:** Evaluating factors influencing early growth of fingerling tiger trout stocked into subalpine lakes and reservoirs on the Grand Mesa Plateau as biocontrol and to diversify recreational angling opportunities.

OBJECTIVES:

Quantify the trophic ecology, growth and survival of juvenile tiger trout stocked into subalpine lakes supporting different species of undesirable fish to help CPW prioritize which lakes receive tiger trout, inform appropriate numbers to stock, and calibrate expectations on the effectiveness of tiger trout as a biological control agent. Informed stocking translates into (1) efficient use of the limited number of tiger trout produced by our hatchery system, (2) a greater chance tiger trout will perform well at the onset of stocking, and (3) more rapid development of a quality fishing opportunity for anglers.

PUBLICATION:

Hansen, A. G., E. T. Cristan, M. M. Moll, M. W. Miller, E. I. Gardunio, and **J. M. Lepak**. 2022. Factors influencing early growth of juvenile tiger trout stocked into subalpine lakes as biocontrol and to enhance recreational angling. Fishes 7:342.

INTRODUCTION:

Many of Colorado's coldwater lakes contain fish species, such as suckers and minnows, which can achieve high densities, provide little value to anglers, compete with managed sport fish, and have the potential to reduce water quality. However, these undesirable fish may be valuable prey items. Sterile fish that have the ability to grow to predatory size quickly and eat the unwanted fish could act as a biological control agent and provide a unique fishing opportunity. Being unable to reproduce, sterile fish can be closely managed through stocking and harvest regulations. Tiger trout, a sterile hybrid between male Brook Trout and female Brown Trout, have the potential to fill this role. Tiger trout have already been stocked in some Colorado lakes.

Our understanding of what tiger trout eat and how well they grow and survive in lakes with different species of undesirable fish remains limited, and should be fully investigated as a management tool. Factors such as the number of tiger trout stocked per acre of lake and the presence of small-bodied minnows versus larger-bodied suckers may affect the ability of tiger trout to grow quickly enough and survive long enough to eat and suppress the population of undesirable fish. Here we report a new manuscript recently published in the journal *Fishes* examining the relative importance of different biotic and abiotic factors influencing the post-stocking performance (feeding ecology and growth) of fingerling tiger trout early in life. The manuscript abstract is below.

MANUSCRIPT ABSTRACT:

Tiger trout (*Salmo trutta* × *Salvelinus fontinalis*) are sterile hybrids often stocked as a biocontrol agent for undesirable fishes and to enhance recreational angling. Yet, how different ecological processes affect their post-stocking performance remain poorly understood. Rapid growth early in life can foster rapid transitions to piscivory, and improve survival. Identifying factors that benefit early growth can help managers optimize tiger trout stocking for meeting multiple fisheries management objectives. Here, we characterized the trophic ecology and growth of tiger trout stocked at varying densities into seven lentic subalpine systems in Colorado, USA. Study systems supported different species of undesirable fish (e.g., minnows or suckers). We used stable isotopes of carbon and nitrogen to quantify trophic relationships among tiger trout and other fishes in each system. We then evaluated several system-specific attributes as predictors for the size of tiger trout at age-1 using a Random Forest model. Stable isotopes demonstrated the potential for resource competition among tiger trout and other fishes, but potential varied by system. Indices of resource competition ranked highest in the Random Forest model, but the stocking density of tiger trout was most important, suggesting that intraspecific competition outweighed interspecific competition in driving early growth. These processes were mediated by system productivity. Thus, stocking density in combination with the realized carrying capacities of systems should be considered when making management decisions for tiger trout.

RESEARCH PRIORITY: **Mercury contamination in sport fish:** Revisiting mercury research from 2014 Annual Report—Predictors of mercury contamination in Colorado sport fish: implications for informing TMDL development and the protection of human and ecological health.

OBJECTIVES:

To prepare and submit a manuscript that identified factors at the landscape scale that are influencing mercury concentrations in Northern Pike, Smallmouth Bass, and Walleye. We also included an evaluation of theoretical changes in mercury deposition and food web structure to compare the magnitude and timing of potential changes in sport fish mercury concentrations from those changes. After two previous rejections, this manuscript is now undergoing revisions for PLOS ONE.

MANUSCRIPT SUBMISSION:

Lepak, J. M., B. M. Johnson, M. B. Hooten, B. A. Wolff, and **A. G. Hansen.** *In revision*. Predictors of sport fish mercury contamination in heavily managed reservoirs: implications for human and ecological health. PLOS ONE.

INTRODUCTION:

Fish consumption advisories associated with mercury contamination have been put in place by the Colorado Department of Public Health and the Environment. The Lake and Reservoir Research Laboratory has provided technical advice for setting these advisories for several years, and multiple research projects have been conducted to address this issue from a food web perspective in Colorado. For example, Lepak et al. (2012a), Lepak et al. (2012b), Stacy and Lepak (2012), Johnson et al. (2015), Lepak et al. (2016), and Wolff et al. (2017) all provide Colorado-specific information about mercury contamination in sport fish and how management may influence mercury concentrations. Continuation of this work at the landscape level for more predictive purposes was made possible by compiling data from across the state and applying a machine learning approach to inform what might be driving mercury concentrations in Northern Pike, Smallmouth Bass, and Walleye. We also evaluated the magnitude and timing of potential changes in sport fish mercury concentrations based on different deposition and food web change scenarios.

MANUSCRIPT ABSTRACT:

Mercury (Hg) is an important contaminant due to its widespread distribution and tendency to accumulate to harmful levels in biota. We used a machine learning approach called random forest (RF) to evaluate different predictors of Hg concentrations in three species of Colorado sport fish. The RF approach indicated that the best predictors of large Northern Pike (*Esox lucius*) Hg concentrations at 864 mm were covariates related to salmonid stocking in each study system, while system-specific metrics related more to productivity and forage base were the best predictors of Hg concentrations of Smallmouth Bass (*Micropterus dolomieu*), and Walleye (*Sander vitreus*) at

381 mm. Importantly, protecting human and ecological health from Hg contamination requires an understanding of fish Hg concentrations and variability across the landscape and through time. The RF approach could be applied to identify potential areas/systems of concern, and predict how sport fish Hg concentrations may change as a result of a variety of factors to help prioritize, focus, and streamline monitoring efforts to effectively and efficiently inform human and ecological health.

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<u>RESEARCH PRIORITY</u>: **Triploid Walleye biology:** Recent advancements from ongoing Colorado State University PhD project on triploid Walleye ecology in collaboration with CPW. Here we report results and short summaries from two new completed dissertation chapters currently in preparation for submission to scientific journals.

OBJECTIVES:

Evaluate the post-stocking performance [trophic ecology, growth, survival, reproductive characteristics (e.g., gonadal development), and population dynamics] of triploid versus diploid Walleye to help inform management and appropriate stocking procedures on the Western Slope of Colorado.

MANUSCRIPT SUBMISSION I:

Farrell, C. J., B. M. Johnson, **A. G. Hansen**, B. W. Avila, and C. A. Myrick. *Submitted*. Does reproduction cause growth deceleration? Growth comparisons between diploid and triploid walleye address a long-standing debate PNAS Nexus.

INTRODUCTION:

It is thought that growth and reproduction are linked, and the assumed tradeoff between them is fundamental to life history theory (Reznick 1985; Lika and Kooijman 2003; Sibly et al. 2015). The nature of this tradeoff has stimulated intense debate in the ecological and evolutionary literature (Kooijman and Lika 2014; Marshall and White 2019) and is regarded as one of the most critical theoretical issues in ichthyology (Pauly 2021). According to evolutionary theory, reproductive effort—the proportion of an organism's energy budget devoted to reproductive processes—is selected for in a way that maximizes fitness, but at a cost to growth in body size (Hirshfield and Tinkle 1975). The most common energy budget models underpinning life history theory assume energy is diverted from potential somatic growth to fuel reproduction (Schaffer 1974; Hirshfield and Tinkle 1975; Tuomi et al. 1983; Perrin and Sibly 1993). This idea, coined as the Reproductive Drain Hypothesis (RDH) by Iles (1974), implies a fixed energy budget (Hirshfield and Tinkle 1975; Tuomi et al. 1983), and is considered by many to be responsible for indeterminate growth patterns (i.e., growth deceleration) in multiple taxa (Roff 1983; Day and Taylor 1997; Charnov et al. 2001; Quince et al. 2008a).

The validity of RDH has been questioned because the synchrony between the onset of growth deceleration and sexual maturation does not imply causation. For example, the Gill-Oxygen Limitation Theory supposes that reproductive development is triggered at a critical oxygen limitation threshold, and is therefore the result, rather than the cause, of growth deceleration (Pauly 1981). Additionally, Pauly (2019) points to the logical conundrum that female fish, which typically invest more energy into reproductive development, are often larger than male conspecifics, counter to expectations under RDH.

In this paper, we test RDH in a novel manner, by comparing the average adult body sizes of a sterile freshwater fish to fertile conspecifics co-occurring in the wild. We examined Walleye effectively sterilized via induced triploidy (Fetherman et al. 2015). Like most fish species, Walleye grow indeterminately (Charnov et al. 2001; Henderson et al. 2003). Additionally, Walleye are iteroparous, capital spawners that typically spawn once per year (Barton and Barry 2011; McBride et al. 2015). Triploid Walleye do not allocate energy toward the production of gametes and are likely less active during the spawning period than fertile diploids (Farrell et al. 2022). Thus, comparisons of growth patterns and maximum body size between triploid and diploid Walleye cohabiting under the same physical, chemical, and ecological conditions are well suited for directly testing RDH (Pauly 2021). Specifically, we fit length-at-age data collected from sympatric sterile and fertile Walleye to the Pütter-von Bertalanffy growth model (P-VBGM; Kearney 2021) and the Lester Biphasic Growth Model (LBGM; Lester et al. 2004) in a hierarchical Bayesian framework using informative prior information. We hypothesized that, if reproduction contributes to growth deceleration, then (1) sterile individuals would grow larger than fertile ones, and would have significantly higher estimates for L_∞, a shared model parameter corresponding to the average maximum total length, and (2) LBGM would receive more model weight for sterile fish than P-VBGM because LBGM explicitly accounts for the energetic costs of reproduction and RDH.

RESULTS & DISCUSSION:

Each sex-by-ploidy group exhibited asymptotic growth over the range of sizes (179–692 mm) and ages (0.54–13.31 years old) examined. Females of both ploidies obtained larger body sizes than males, a common pattern observed for Walleye and may reflect evolutionary pressures to maximize reproductive output with minimal parental care (Hirshfield and Tinkle 1975; Bozek et al. 2011). We did not find evidence to support our first hypothesis that, if RDH governs body size, sterile fish would be larger than fertile fish (*e*-value = 0.08). Estimates of L_∞ for P-VBGM were similar between fertility statuses within each sex, but females were larger than males regardless of fertility.

Overall, the P-VBGM fit all groups well, whereas LBGM fit fertile fish well, but not sterile fish. We found that LBGM (model weight = 0.795) described the length-at-age of fertile Walleyes better than P-VBGM (model weight = 0.205). This finding aligns with previous work showing that biphasic models outperform uniphasic ones for fertile fish (Quince et al. 2008b; Armstrong and Brooks 2013; Minte-Vera et al. 2016), which has lent credence to RDH and helped fuel the ongoing debate of reproduction's role in limiting growth. However, we found that RDH could not explain growth for sterile Walleye (LBGM model weight = 0.049), which brings into question the validity of RDH and points to the importance of alternative energy budget models, like assimilation models. Residual plots showed that LBGM overestimated the size of younger and older fish. Counter to expectations under RDH, our results indicate that the growth of sterile fish is asymptotic and better characterized by the P-VBGM (model weight = 0.951).

Our findings indicate that reproduction does not drive growth deceleration, contrary to RDH. The LBGM, a model with RDH as a key assumption, could not characterize the asymptotic nature of body size observed for sterile Walleye that invest little to no energy into reproduction. Under RDH, we expected L_∞ estimated for sterile Walleye to exceed fertile Walleye, but estimates were nearly identical for fish growing under equivalent physical, chemical, and ecological conditions.

Furthermore, the LBGM represented the growth patterns of sterile Walleye poorly, as it received only 4.1% of model weight in contrast to 95.9% assigned to P-VBGM. Lastly, female Walleye, regardless of fertility, obtained larger maximum body sizes than males. This finding is difficult to explain under the assumption of RDH (Pauly 2019; Pauly 2021), as female Walleye in this population allocate, on average, 1,756% more energy to gamete production than males by 8 years old (Farrell et al. 2022). Since sexually dimorphic growth was also conserved in sterile Walleye, processes other than reproduction must drive ultimate body size. Thus, growth trajectories of sterile fish are likely better explained by a combination of inheritance and metabolic theory (White et al. 2022).

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MANUSCRIPT SUBMISSION II:

Farrell, C. J., B. M. Johnson, **A. G. Hansen**, and C. A. Myrick. *In prep*. Relative performance of juvenile triploid Walleye in the wild. Target journal: North American Journal of Fisheries Management.

INTRODUCTION:

The artificial induction of triploidy has been frequently used in finfish and shellfish commercial aquaculture (Benfey 1999; Piferrer et al. 2009) and to produce Grass Carp *Ctenopharyngodon idella* for aquatic vegetation control (Allen and Wattendorf 1987). The primary motivation for using triploid fish is because they are sterile, which reduces the risk of unwanted reproduction and genetic introgression should stocked fish disperse from their desired locale (Benfey 1999; Piferrer et al. 2009). Interest in using triploid fish has risen among sport fisheries managers because they provide a lower-risk stocking option and may help (1) reconcile sportfish management with native species conservation in some regions (Martinez et al. 2009; Budy et al. 2012; Cassinelli et al. 2019), and (2) reduce propensity for illegal stocking (Johnson et al. 2009).

Triploid Walleye *Stizostedion vitreum* (see Bruner 2021) have been stocked by fisheries management agencies in Colorado, Utah, Montana, and Alberta since as early as 2008. Walleye management in the Colorado and Utah portions of the upper Colorado River basin, USA, emphasizes a suite of measures to reconcile nonnative sport fishing with the recovery of threatened and endangered fish endemic to the Colorado River and its tributaries. This includes stocking triploids to diversify recreational angling opportunities, deter illegal fish stocking, limit the possibility of new populations of Walleye in sensitive areas, and possibly interfere with reproduction in unwanted diploid populations (Johnson et al. 2009; Farrell et al. 2022a). Within the upper Colorado River basin, Colorado Parks and Wildlife stocks triploid Walleye into Narraguinnep, Rifle Gap, and Puett reservoirs, and Utah Division of Natural Resources stocks triploid Walleye into Red Fleet and Big Sand Wash reservoirs (Robert Shields, Utah Division of Wildlife Research, personal communication). Outside of the upper Colorado River basin, triploid Walleye are typically stocked to limit unwanted introgression with native *Stizostedion* species. In Montana, triploid Walleye have been stocked in Bighorn Reservoir semi-regularly since 2009 to prevent hybridization with native Sauger *Stizostedion canadanse* (Bramblett and Zale 2016; S. Blackburn, Montana Fish, Wildlife, and Parks, personal communication). In Alberta, triploid Walleye were stocked into Lac Ste. Ann in 2021 to reduce the risk of introgression with wild Walleye already present in the system (S. Fithen, Alberta Environment and Parks, personal communication). While this describes most extant triploid Walleye populations and stocking programs, there is interest in expanding triploid Walleye stocking throughout the western U.S. and Canada.

Despite growing interest in stocking triploid Walleye, there is a lack of basic information regarding their post-stocking performance. Managers need to know more about how growth and survival of triploids compares to diploid conspecifics in order to use triploid Walleye effectively, especially given their increasing use as an alternative stocking method. In this study, we used three years of paired stocking events of diploid and triploid Walleye in two Colorado reservoirs to evaluate the performance of triploid Walleye early in life. Specifically, we investigated relative differences in growth and survival between multiple cohorts of triploid and diploid Walleye.

METHODS:

Jumbo (40.93ºN, 102.65ºW) and Jumbo Annex (40.91ºN, 102.665ºW) reservoirs are water storage impoundments west of Sedgwick, Colorado, USA. The primary water source for these reservoirs is the South Platte River. Jumbo Reservoir has a maximum surface area of 639 ha and maximum depth of approximately 7 m at full pool (surface elevation of 1,131). Jumbo Annex Reservoir has a maximum surface area of 32 ha and maximum depth of approximately 4.5 m at full pool (surface elevation = 1,125 m). Both reservoirs have fish communities composed of Walleye, saugeye (Walleye *Stizostedion vitreum* × Sauger *S*. canadense), Black Crappie *Pomoxis nigromaculatus*, White Crappie *Pomoxis annularis*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass, Channel Catfish *Ictalurus punctatus*, Yellow Perch *Perca flavescens*, Bluegill *Lepomis macrochirus*, Green Sunfish *Lepomis cyanellus*, Orange Spotted Sunfish *Lepomis humilis*, wiper (White Bass *Morone chrysops* × Striped Bass *M. saxatilis*), Gizzard Shad *Dorosoma cepedianum*, and Freshwater Drum *Aplodinotus grunniens*.

Paired stocking of triploid and diploid Walleye fry and fingerlings combined of known densities occurred each spring 2018–2021, except for 2020, when no Walleye were stocked due to the COVID-19 pandemic. Walleye were produced, ploidy was verified, and stocking densities were estimated according to the methods described by Fetherman et al. (2015). At Jumbo Reservoir, diploid and triploid fry were stocked at 1,902–6,293 fish/ha and diploid and triploid fingerlings at 15–47 fish/ha across years. At Jumbo Annex Reservoir, diploid and triploid fry were stocked at 1,563–5,859 fish/ha, and diploid and triploid fingerlings at 30–63 fish/ha across years (Table 1).

Target sizes of fish kept for biological sampling depended on sampling year and prior system-specific knowledge of Walleye growth rate. In 2018, we targeted only age 0 Walleye, and sampled all fish <300 mm total length (TL). In 2019, we targeted age 0 and age 1 Walleye and sampled all fish <400 mm. In 2020 and 2021, we targeted up to age-4 Walleye, which required sampling of all fish encountered <500 mm. Prior to biological sampling, fish were euthanized with MS-222 (250 mg/L). Sampled fish were measured for TL and weighed (WW; g). A blood sample, obtained via cardiac puncture (Duman et al. 2019), and/or a caudal fin clip was collected from each individual for ploidy determination using methods described by Farrell et al. (2022b). Sagittal otoliths were collected from each fish for age determination.

Otoliths were sectioned transversely through the core, placed on a slide, immersed in mineral oil to enhance readability, and photographed using a camera mounted to a compound microscope at 40–100x magnification under reflected light. An experienced reader (C. Farrell) aged each fish three times using the package RFishBC in R (Ogle 2019). Fish for which all three age assignments corresponded were used to create system-, ploidy-, and year-specific age-length keys to apply to unaged fish and for fish which had disagreeing age assignments using the package FSA (Ogle et al. 2022). We calculated age as the time elapsed from birth until capture, assuming fish were born on April 1st of their estimated birth year (Barton and Barry 2011).

All statistical analyses were performed using R 4.1.3 (R Development Core Team 2022). We used package brms, a high-level interface to stan, to fit growth and relative survival models (see below) in a Bayesian framework (Bürkner 2017; Bürkner 2018; Bürkner 2021). Each model was fit by implementing four chains of length 3,000 using brms and the No-U-Turn sampler (Hoffman and Gelman 2014). For each chain, the first 1,500 iterations were discarded as burn-in, leaving 6,000 draws to make inference on the posterior distribution of each model's parameters. We used default priors provided by brms for all models. Convergence of chains was assessed using the potential scale reduction factor ($\hat{r}$) with estimates less than 1.05 considered acceptable and demonstrating convergence (Vehtari et al. 2021). Figures were created using packages ggplot2 (Wickham 2016) and tidybayes (Kay 2022).

We tested for differences in length-at-age between triploid and diploid Walleye by comparing the predicted posterior distributions of TL for each age-class (i.e., 0–3) on October 1. To account for multiple sampling events within a given year, we estimated the posterior distribution of TL for diploid and triploid Walleyes using the following hierarchical model:

$$\mathrm{TL}_{t_i} \sim lognormal(\mu, \sigma) \tag{1}$$

$$\mu = \log(a_i - b_i t) \tag{2}$$

$$a_i \sim N(0, \sigma) + (1|cohort + waterbody) \tag{3}$$

$$b_i \sim N(0, \sigma) + (1|cohort + waterbody) \tag{4}$$

where TL_{ti} is the total length (mm) of ploidy *i* and fractional age *t*, with random intercepts (*a*) and slopes (*b*) for each cohort and waterbody from separate regressions for each age-class. We used posterior draws for *a* and *b* to calculate the posterior predictive distribution for diploid and triploid fish at $t = 0.5$, 1.5, 2.5, and 3.5. We used Full Bayesian Evidence Testing (Pereira and Stern 1999), which is a Bayesian analog to classical *p*-value hypothesis testing, to quantitatively test our null hypotheses that there were no differences in growth within age-classes between ploidies. Differences <5% were considered not different. Full Bayesian Evidence Tests produce *e*-values, which is the epistemic value of a hypothesis given the observed data, similar to a *p*-value in the frequentist realm (Pereira and Stern 2022). We used package fbst (Kelter 2022) to calculate e-values to test our hypotheses. We set an interval of ±5% for our null hypothesis that there was no difference in the percent difference (i.e., $100 \times [\mathrm{TL}_{\mathrm{triploid}} - \mathrm{TL}_{\mathrm{diploid}}] / \mathrm{TL}_{\mathrm{diploid}}$) in posterior means of TL at age *t* between triploid and diploid Walleye.

The survival of triploid and diploid Walleye was assessed in relative terms. According to Hilborn and Walters (1992), catch is proportional to abundance:

$$C_t = qE_tN_t \tag{5}$$

where C_t is catch at time *t*, *q* is the catchability coefficient, E_t is fishing effort at time *t*, and N_t is abundance at time *t*:

$$N_t = N_{t-1}s \tag{6}$$

where *s* is the survival rate from *t*-1 to *t*. Assuming *q* does not differ by ploidy, and because *E* did not differ between ploidies of the same cohort and age, we estimated the ratio of survival of triploids relative to diploids as:

$$\frac{S_{3N_{ijt}}}{S_{2N_{ijt}}} = \frac{C_{3N_{ijt}} C_{3N_{ij(t-1)}}}{C_{2N_{ijt}} C_{2N_{ij(t-1)}}} \tag{7}$$

where $\frac{S_{3N_{ijt}}}{S_{2N_{ijt}}}$ is the ratio of triploid (3N) to diploid (2N) survival for cohort *i* in reservoir *j* at age *t*, $\frac{C_{3N_{ijt}}}{C_{2N_{ijt}}}$ is the ratio of catch for cohort *i* in lake *j* at age *t*, and $\frac{C_{3N_{ij(t-1)}}}{C_{2N_{ij(t-1)}}}$ is the ratio of catch for cohort *i* in lake *j* at age *t*-1. To estimate relative survival at age *t* = 0.5, we used estimated (by hatchery) stocking numbers of diploid to triploid Walleye to compute the ratio of the catch at age *t*-1. Because we could not account for the origin (i.e., natural versus stocked) or the size-at-stocking (fry versus fingerling), we ran two scenarios to estimate the relative difference of survival from stocking to the first fall of age 0 fish—we assumed that all fish captured in the fall were either 100% fry or 100% fingerlings to bracket the range of potential relative survivals driven by size-at-stocking.

We estimated the posterior distributions of relative survival for diploid and triploid Walleyes using the following Bayesian model:

$$\frac{S_{3N_{ijt}}}{S_{2N_{ijt}}} \sim lognormal(\mu, \sigma) \tag{8}$$

where μ is analogous to the intercept. Posterior distributions of relative survival where the highest density interval (HDI) overlapped 1.0 (i.e., relative survival of triploid fish = diploid fish) were considered not significantly different, whereas those that had HDIs not overlapping 1.0 were considered significantly different.

RESULTS:

Over four years of sampling, we collected 2,788 Walleye (Table 2), of which 320 were unaged due to missing or low-quality otoliths. Age estimation was precise; there were disagreeing ages for only 77 fish among otoliths with three age reading replicates (*n* = 2,391). Cohorts present in our sample ranged from 2009–2021: 871 fish belonged to cohorts outside of our stocking window (i.e., 2009–2017), and 1917 belonged to cohorts within our stocking window (i.e., 2018–2021).

TL-at-age

For age 0 fish, posterior means for the parameters of the hierarchical linear model for diploids were a = 71.7 (σ = 8.9) and b = 290.0 (σ = 17.1). For triploids, a = 71.4 (σ = 17.3) and b = 259.3 (σ = 35.5). Posterior predicted mean TL at t = 0.5 was 217 mm (95% HDI = 183–254 mm) for diploids and 201 mm (170–236 mm) for triploids (Figure 1). The posterior mean of the difference in TL at t = 0.5 between ploidies was 15.6 mm (12.5–18.9 mm). Thus, triploids were 7.2% smaller on average than diploids at t = 0.5, with an *e*-value <0.01, meaning that the probability of no difference in mean TL (according to our *a priori* criteria) was <0.01 (Figure 1).

For age-1 fish, posterior means for the parameters of the hierarchical linear model for diploids were a = 68.1 (σ = 30.3) and b = 174.4 (σ = 21.4). For triploids, a = 162.7 (σ = 59.6) and b = 100.5 (σ = 40.3). Posterior predicted mean TL at t = 1.5 was 329 mm (95% HDI = 286–376 mm) for diploids and 313 mm (271–360 mm) for triploids (Figure 1). The posterior mean of the difference in TL at t = 1.5 was 16.3 mm (11.2–21.0 mm). Thus, triploids were 4.9% (3.4–6.5%) smaller on average than diploids at t = 1.5, but the *e*-value was 0.528, so this difference was not significant (Figure 1).

For age-2 fish, posterior means for the parameters of the hierarchical linear model for diploids were a = 436.8 (σ = 166.2) and b = -17.1 (σ = 67.2). For triploids, a = -61.4 (σ = 519.2) and b = 173.2 (σ = 207.5). Posterior predicted mean TL at t = 2.5 was 393 mm (95% HDI = 324–467 mm) for diploids and 370 mm (306–445 mm) for triploids (Figure 1). The posterior mean of the difference in TL at t = 2.5 was 27.4 mm (13.2–42.6 mm). Thus, triploids were 6.3% (2.8–9.7%) smaller on average than diploids at t = 2.5, but this difference was not significant as the e-value was 0.267 (Figure 1).

For age-3 fish, posterior means for the parameters of the hierarchical linear model for diploids were a = -807 (σ = 698) and b = 354 (σ = 119). For triploids, a = -1109.6 (σ = 2231) and b = 433 (σ = 636). Posterior predicted mean TL at t = 3.5 was 436 mm (95% HDI = 368–505 mm) for diploids and 408 mm (345–479 mm) for triploids (Figure 1). The posterior mean of the difference in TL at t = 3.5 was 22.5 mm (13.7–31.3 mm). Thus, triploids were 5.7% (3.6–8.1%) smaller on average than diploids at t = 3.5, but this difference was not significant as the e-value was 0.230.

Relative survival

In all years, the proportion of age 0 triploids was lower than age 0 diploids from stocking to the first fall (i.e., t = 0.5), but we did not observe changes in relative catch between ploidies at subsequent ages (Figure 2). When assuming that all age 0 Walleye captured in the fall were stocked as fry, the median of the posterior distribution for the ratio of survival of triploids to diploids was 0.21 (95% HDI = 0.04–0.48). When assuming that all age-0 Walleye captured in the fall were stocked as fingerlings, the median of the posterior distribution for the ratio of survival of triploids to diploids was 0.23 (0.05–0.49). These estimates were combined across cohorts and study systems. Because the HDIs for both post-stocking scenarios did not overlap 1.0, survival for age 0 triploids was significantly lower than diploids from stocking to their first fall (Figure 3). The ratios of survival beyond age 0 were not significantly different, as 95% HDIs for other age-classes (1-3) each overlapped 1.0 (Figure 3). The median of the posterior distribution for the ratio of survival of triploids to diploids was 1.25 (0.16–3.15) for age 1 fish, 0.66 (0.06–1.91) for age 2 fish, and 1.45 (0.01–6.83) for age 3 fish.

DISCUSSION:

This study is the first to assess the growth and relative survival of juvenile triploid Walleye in the wild. Overall, we found that age 0 triploid Walleye were significantly smaller (8%) and had significantly lower survival on average (77–79%) than age 0 diploid Walleye. However, there were no significant differences in size or survival between triploid and diploid Walleye at ages 1–3.

Differences in size between ploidies of age 0 Walleye may be explained by several factors. Growth of fish, especially during the juvenile stages, tends to be shaped by metabolism (Kooijman 2010; Kearney 2021). The Gill-Oxygen Limitation theory (Pauly 1981) posits that metabolism, and thereby growth, in immature water-breathing ectotherms is proportional to oxygen uptake Q:

$$Q = \frac{dP \times U \times GSA}{WBD} \tag{9}$$

where dP is the difference between the oxygen partial pressure on either side of the gill membrane, U is Krogh's diffusion constant, GSA is the gill surface area, and WBD is the water-blood distance, or the thickness of the gill tissue separating water and blood. Sadler et al. (2001) found that triploid Atlantic Salmon *Salmo salar* had reduced gill surface areas relative to diploid controls, which could correspond to relatively lower oxygen uptake and growth rates for triploids. Also, it may be possible that triploid growth could be limited because they may have a relatively larger water-blood diffusion distance (Benfey 1999). Triploids have 50% more DNA than diploids, and have larger cells to accommodate their larger genome, which would correspond to larger diffusion distances and reduced growth (Benfey 1999).

It is also possible that triploid Walleye have narrower thermal tolerances than diploid Walleye, as has been demonstrated for triploids of other species (Altimiras et al. 2002; Fraser et al. 2012b; but see Bowden et al. 2018). This could negatively affect their food consumption and growth rates (Kitchell et al. 1977). Maximum surface temperatures in Jumbo and Jumbo Annex were typically around 26°C, which is higher than the optimal temperature for consumption of larval and juvenile walleye (25ºC), but below their maximum temperature for consumption (28ºC) and respiration (32ºC; Madon and Culver 1993). If triploid Walleye have lower thermal tolerances, surface temperatures at Jumbo and Jumbo Annex could lead to relatively lower growth for triploid Walleye at these life stages.

Survival is often size-dependent, with smaller fish generally more susceptible to predation, cannibalism, and starvation (Miller et al. 1988). Grausgruber and Weber (2020) found that the probability of an age 0 Walleye being preyed upon decreased by 2% for every 10 mm increase in TL. According to their findings, we would expect that triploid Walleye have 3.1% (95% HDI: 2.5–3.8%) increased chance on average of being the victim of predation compared to diploids.

There are several other potential explanations for the lower relative survival rates observed for age 0 triploid Walleye. It is possible that triploid Walleye have more morphological abnormalities compared to diploids. For example, compared to diploids, triploid Atlantic Salmon were more susceptible to deformities of the jaw (Sutterlin et al. 1987), had higher prevalence of vertebral deformities (Fjelldal and Hansen 2010), and exhibited altered brain morphology (Fraser et al. 2012a), all of which could negatively affect relative survival of larval triploid fish. It is also possible that triploids are less well-suited to dealing with the natural environment, as triploids can be less aggressive than diploids, and more susceptible to thermal stress, both of which could negatively affect triploid survival (Fraser et al. 2012b). For *Stizostedion spp.,* Czesny et al. (2002) demonstrated that triploid Saugeye were less aggressive and less successful predators than diploids in controlled feeding experiments. As hypothesized by Koch et al. (2018), less successful foraging by triploids could negatively affect growth, exposing them to more predation pressure resulting in reduced survival.

Producing triploid fish is time sensitive and production-related issues could also explain low post-stocking survival. For example, Fetherman et al. (2015) found that adjusting time to initiation of pressurization of fertilized eggs by only 3.5 minutes led to nearly 3-fold higher hatching rates. While unknown, it is possible that small differences in time to pressurization post-fertilization could also affect post-stocking survival. Also, Taylor et al. (2011) demonstrated that egg quality was more indicative of hatching success in Atlantic Salmon than ploidy status. Post-ovulatory oocyte ageing has been identified as the most important factor affecting fish egg quality (Samarin et al. 2019), and egg quality may also explain variability in recruitment in the wild (Kjørsvik et al.

1990). Thus, increased handling time required for triploid production may increase oocyte ageing and could be one explanation for the low relative survival of age 0 triploid Walleye observed in this study.

The lower relative survival rate observed for age 0 triploid Walleye were not observed in the older age 1 to age 3 fish, indicating that there may be an early period of high mortality for triploids during their first year of life that could act as a recruitment bottleneck. Interestingly, triploid fish generally show similar if not lower mortality rates than diploids beyond the larval stages (Fraser et al. 2012b). We may expect this early period of higher mortality to be more pronounced at the fry stage of triploids, rather than the fingerling stage, which could help explain the consistent drop in the relative catch of age 0 triploid fish during their first fall in this study. Post-stocking survival of diploid Walleye typically increases with age-at-stocking (Fielder 1992; Johnson et al. 1996; Weber et al. 2020). Stocking of older juvenile triploids, like fingerlings or advanced fingerlings, could lead to improved triploid Walleye recruitment (Fraser et al. 2012b). Diploid Walleye stocked as fry can also experience high rates of mortality, with <0.2% surviving to their first fall (McWilliams and Larscheid 1992; Brooks et al. 2002).

Fingerling Walleye typically have higher survival rates than those stocked as fry (Fielder 1992; Koppelman et al. 1992; Grausgruber and Weber 2020). Johnson et al. (1996) found that for Walleye stocked as fingerlings, survival to their first fall was approximately 2.5% on average. Existing studies on triploid *Stizostedion spp.* fry found that triploids had low relative survival rates (Ewing 1989; Garcia-Abiado et al. 2002; Koch et al. 2018), but the post-stocking survival for triploid saugeye planted as fingerlings was similar to diploids (Garcia-Abiado et al. 2002). Walleye fry are typically stocked within days of hatching, and prior to the onset of exogenous feeding (Barton and Barry 2011; Kerr 2011). Larval triploid fish often exhibit higher rates of deformities and reduced sensory capacity relative to diploids (Maxime 2008), both of which could reduce survival relative to diploids. As such, triploid Walleye stocked as fry may experience higher mortality rates in the days or weeks following stocking, whereas triploid Walleye stocked as fingerlings may have already gone through this "mortality filter" during the hatchery production process. Unfortunately, we were unable to determine the age-at-stocking for sampled fish and unable to disentangle its impact on this experiment. Future studies should focus on evaluating potential stage-specific differences in survival for triploid Walleyes.

Our estimates of relative survival for age 0 may be biased against triploid Walleye, as we could not account for the origin of diploid Walleye (i.e., natural origin versus hatchery). If natural reproduction occurred during our study, relative survival estimates would be biased against triploid fish, because there could have been more age 0 diploids present at the time of sampling than otherwise expected. We have evidence that natural reproduction occurred in both of our study reservoirs in 2020, as no Walleye (diploid or triploid) were stocked, but we captured three age 0 diploid Walleye at Jumbo Reservoir and 43 age 0 diploid Walleye at Jumbo Annex Reservoir that fall.

Overall, our results are encouraging for the use of triploid Walleye as an alternative stocking method. Growth and survival for age 1+ triploid Walleye was not significantly different than diploid Walleye, indicating that if early ecological bottlenecks could be avoided by stocking fingerlings or advanced fingerlings, then triploids may effectively recruit to the fishery. Triploid

Walleye are useful in situations where unwanted natural reproduction is a concern (Bramblett and Zale 2016; Koch et al. 2018; Farrell et al. 2022a). In addition, stocking triploid fish to provide a desirable sport fishing opportunity may help deter illegal stocking and also decrease the chances of the illegal movement of reproductive fish as discerning ploidy visually by anglers using external characteristics is implausible (Benfey 1999; Johnson et al. 2009). Further, adult triploid Walleye are more efficient predators than diploid Walleye. The trophic efficiency of triploid Walleye decreases contaminant bioaccumulation, making them especially appealing for stocking in systems where contaminant problems exist (Farrell et al. 2022a). The trophic efficiency of triploid Walleye could also potentially allow for a system to support higher Walleye densities, meaning more large fish for anglers to catch. This study also provides a foundation for more research aimed at clarifying differences in survival during their first year of life. More detailed studies are needed to address a potential bottleneck in triploid Walleye recruitment by investigating stage-specific survival of larval triploid Walleye.

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TABLES & FIGURES:

Table 1. Total numbers and stocking densities (number/ha) of fry and fingerling triploid (3N) and diploid (2N) Walleye at Jumbo (JUM) and Jumbo Annex (ANX) reservoirs, 2018–2021.

			Fry		Fingerling	
Waterbody	Cohort	Ploidy	*N*	Density (*N*/ha)	*N*	Density (*N*/ha)
ANX	2018	2N	50,000	1562.5	1,042	32.6
		3N	50,382	1574.4	974	30.4
	2019	2N	138,692	4334.1	1,998	62.4
		3N	161,353	5042.3	2,002	62.6
	2021	2N	222,664	6958.3	2,017	63.0
		3N	152,336	4760.5	2,006	62.7
JUM	2018	2N	1,584,414	2479.5	10,006	15.7
		3N	1,686,414	2639.1	9,984	15.6
	2019	2N	1,436,181	2247.5	10,004	15.7
		3N	1,751,252	2740.6	10,008	15.7
	2021	2N	4,153,055	6499.3	30,035	47.0
		3N	2,727,559	4268.5	10,029	15.7

Note: No Walleye were stocked in 2020 at Jumbo or Jumbo Annex due to COVID-19.

Table 2. Age- and cohort-specific total catch (*N*) and corresponding percent triploid ($\%_{3N}$) for all fall sampling events and gear types (i.e., gill netting and electrofishing) targeting diploid and triploid Walleye in Jumbo and Jumbo Annex reservoirs, Colorado, 2018–2021.

		2018 Cohort		2019 Cohort		2020 Cohort		2021 Cohort	
Waterbody	Age	*N*	$\%_{3N}$	*N*	$\%_{3N}$	*N*	$\%_{3N}$	*N*	$\%_{3N}$
ANX	0	23	34.8	249	16.1	43	0.0	161	10.6
	1	67	38.8	55	20.0	35	0.0	-	-
	2	13	30.8	102	21.6	-	-	-	-
	3	32	62.5	-	-	-	-	-	-
JUM	0	178	3.9	450	17.6	3	0.0	121	2.5
	1	73	12.3	75	9.3	1	0.0	-	-
	2	42	2.4	129	10.1	-	-	-	-
	3	42	2.4	-	-	-	-	-	-

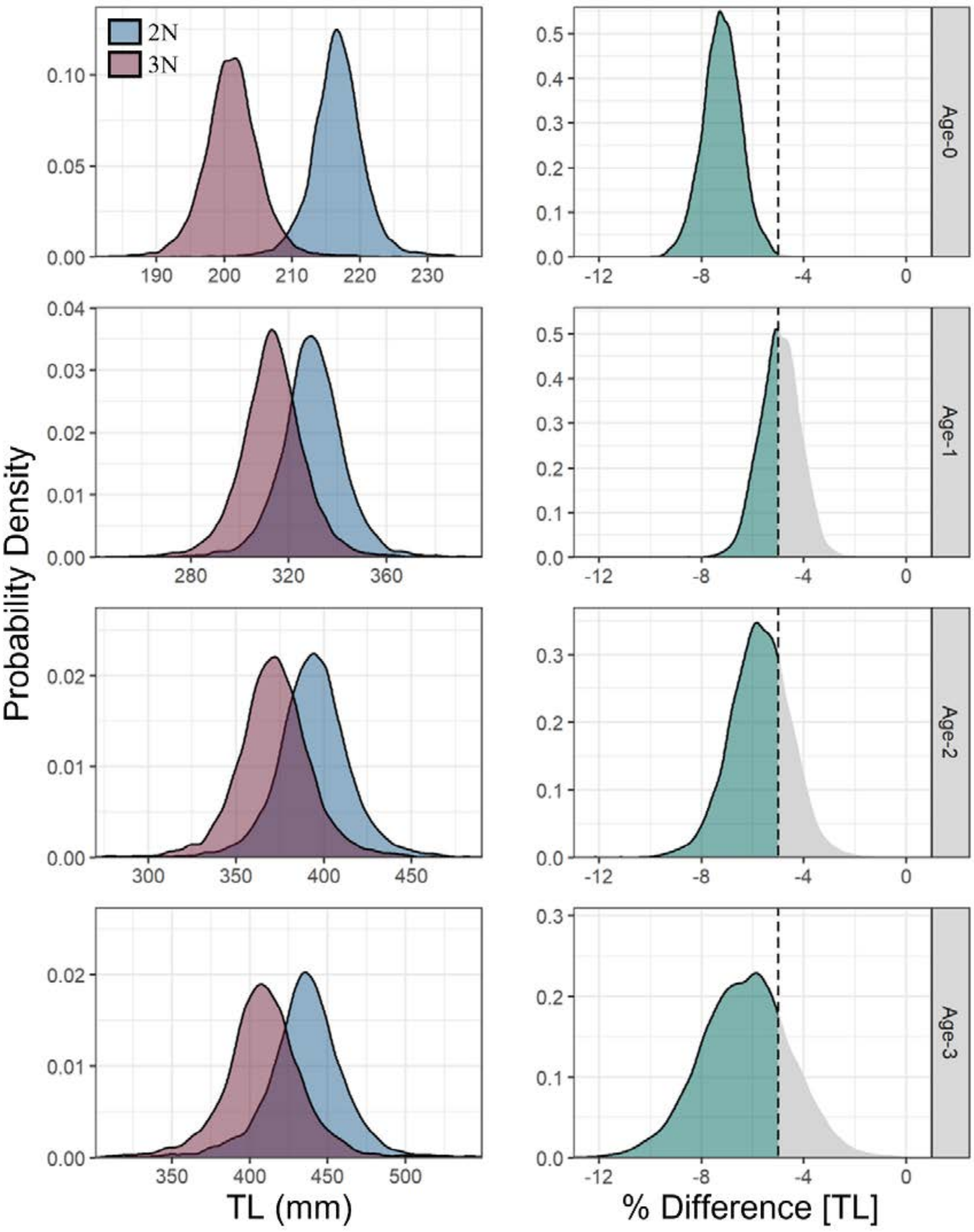

Figure 1. Posterior distributions of mean total length (TL) of diploid (2N) and triploid (3N) Walleye at different ages, and the corresponding distribution of percent differences in TL (i.e., [3N–2N]/2N × 100) between ploidies (Jumbo and Annex reservoirs combined). Each row corresponds to an age-class (i.e., age 0–age 3). For the percent difference plots, the grey shaded area represents our *a priori* criteria of ±5% for no difference in mean TL-at-age *t* between triploid and diploid Walleye and the dashed line denotes a -5% difference for reference.

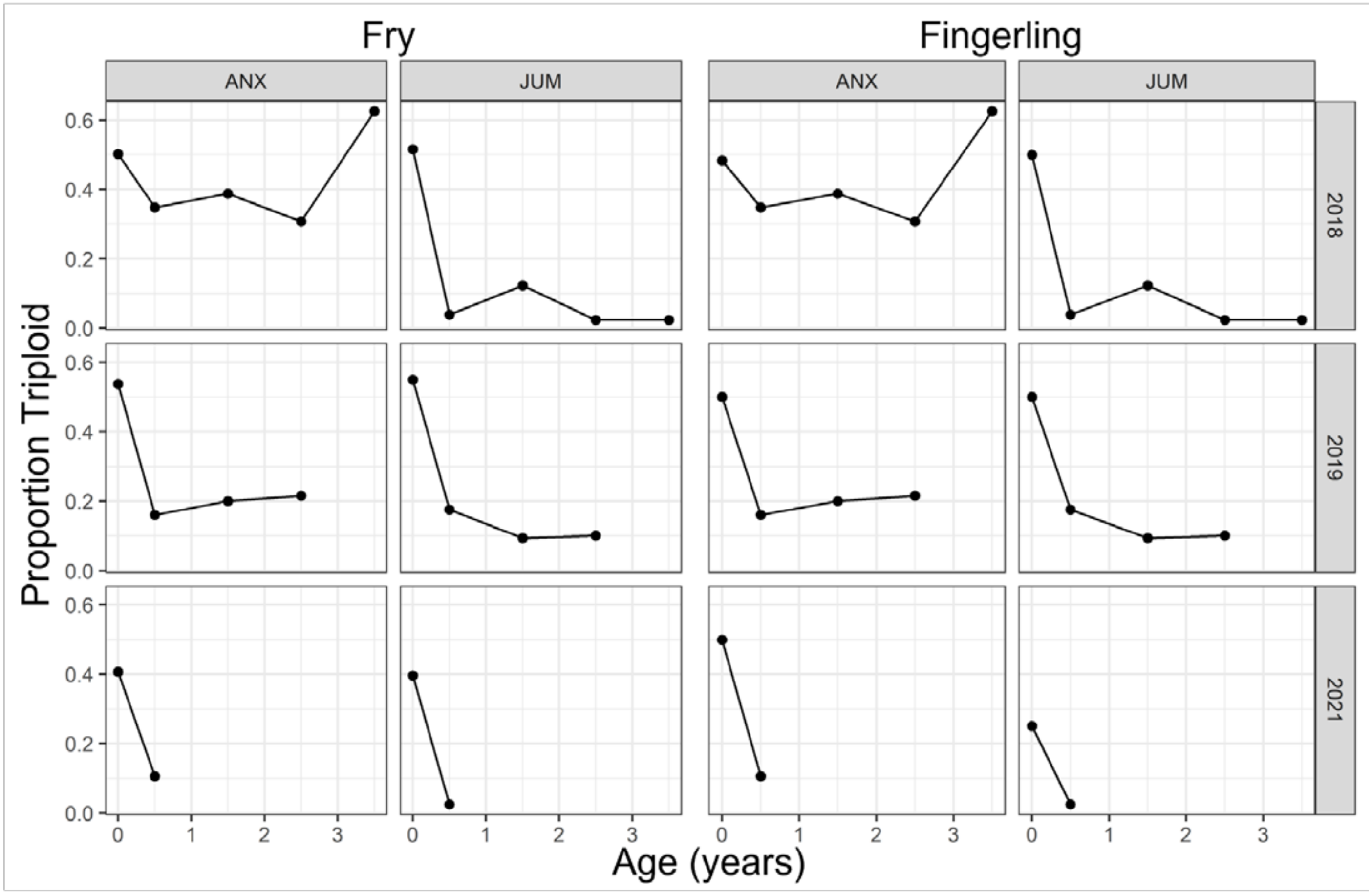

Figure 2. Observed catch proportions of triploids by cohort and age-class at Jumbo Annex (ANX) and Jumbo (JUM) reservoirs (all gears combined) from 2018–2021. The two left columns (Fry) assume that all fish captured at $t = 0.5$ were stocked as fry, and the right two columns (Fingerling) assume that all fish captured at $t = 0.5$ were stocked as fingerlings. Rows represent cohorts.

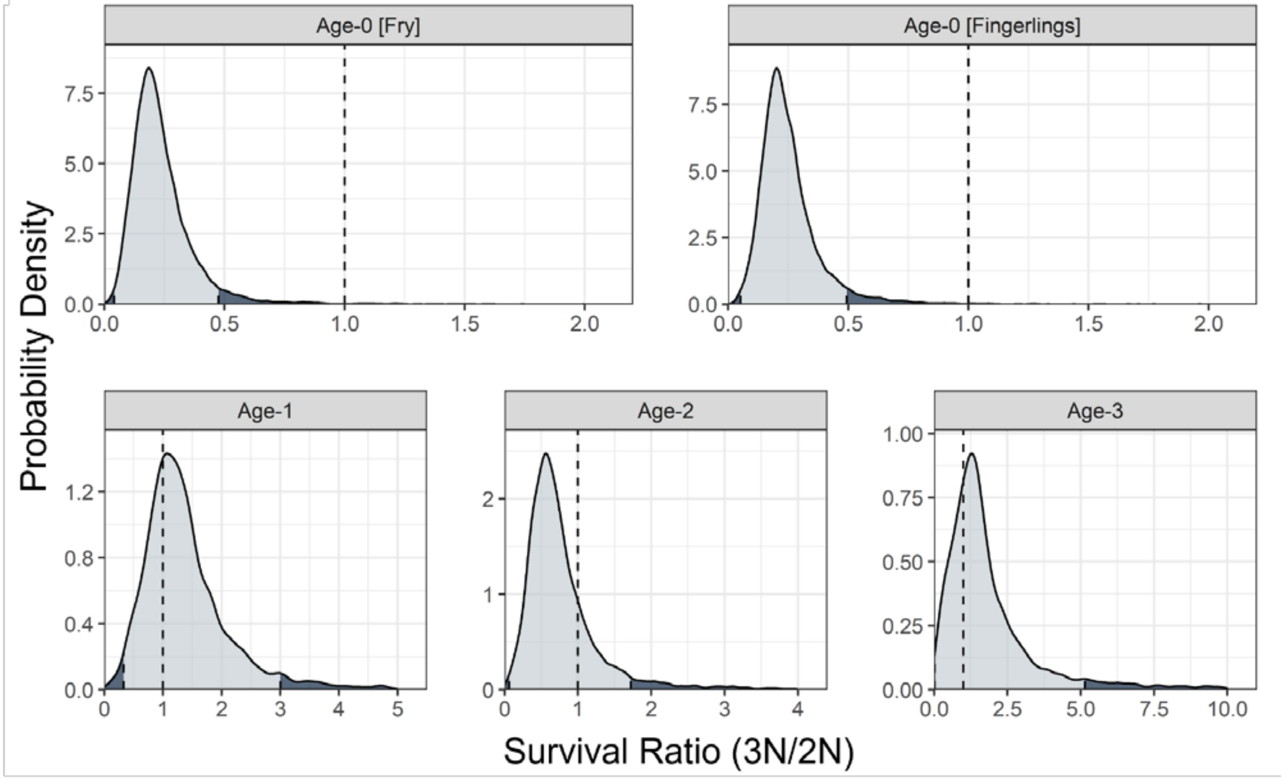

Figure 3. Posterior probability density distributions of the estimated survival ratio of triploid (3N) relative to diploid (2N) Walleye. The light blue shaded area represents the 95% Highest Density Interval (HDI). The dashed line is at 1.0, which represents equivalent survival between triploid and diploid Walleye. Survival ratios that have 95% HDIs which do not overlap the dashed line are considered significantly different. Estimates have been combined across cohorts and study systems.

RESEARCH COMMUNICATION & TECHNICAL ASSISTANCE

Reporting period: December 2021 – November 2022.

Peer-Reviewed Publications:

- Guo, C., L. Shiqi, L. Wei, C. Liao, T. Zhang, J. Liu, L. Li, J. Sun, X. Cai, and **A. G. Hansen**. 2022. Spatial variation in the composition and diversity of fishes inhabiting an artificial water supply lake, Eastern China. Frontiers in Ecology and Evolution 10:921082.

- **Hansen, A. G.**, E. T. Cristan, M. M. Moll, M. W. Miller, E. I. Gardunio, and J. M. Lepak. 2022. Factors influencing early growth of juvenile tiger trout stocked into subalpine lakes as biocontrol and to enhance recreational angling. Fishes.

Manuscripts Submitted for Publication:

- Farrell, C. J., B. M. Johnson, **A. G. Hansen**, B. W. Avila, and C. A. Myrick. *Submitted*. Does reproduction cause growth deceleration? Growth comparisons between diploid and triploid walleye address a long-standing debate. PNAS Nexus.

- Guo, C., L. Shiqi, K. Jie, L. Chuansong, **A. G. Hansen**, E. Jeppesen, Z. Tanglin, L. Wei, and L. Jiashou. *In revision*. Small-bodied zooplanktivorous fishes induce stronger top-down effects on plankton and water quality than omnivorous fishes in shallow subtropical lakes. Water Research.

- **Hansen, A. G.**, A. K. McCoy, G. P. Thiede, and D. A. Beauchamp. *In revision*. Pelagic food web interactions in an invaded ecosystem: implications for reintroducing a native top predator. Ecology of Freshwater Fish.

- Lepak, J. M., B. A. Wolff, B. M. Johnson, M. B. Hooten, and **A. G. Hansen**. *In revision*. Predicting sport fish mercury contamination in heavily managed reservoirs: implications for human and ecological health. PLOS ONE.

External Presentations:

- Farrell, C. J., B. M. Johnson, **A. G. Hansen**, B. W. Avila, and C. A. Myrick**.** Does reproduction limit lifetime growth? Evidence from a population of mixed-ploidy Walleye. PERCIS V. September 25, 2022. České Budějovice, Czechia.

- Farrell, C. J., B. M. Johnson, **A. G. Hansen**, B. W. Avila, and C. A. Myrick**.** Does reproduction limit lifetime growth? 152nd Meeting of the American Fisheries Society. August 25, 2022. Spokane, WA.

- **Hansen, A. G.**, and D. Brauch. Achieving coexistence: a case history of Colorado's premier kokanee-Lake Trout fishery. 152nd Meeting of the American Fisheries Society. August 25, 2022. Spokane, WA.

- Beauchamp, D. A., R. Johnson, B. Jensen, and **A. G. Hansen**. Environmental and ecological constraints on smolt production for salmonids introduced above dams. 152nd Meeting of the American Fisheries Society. August 23, 2022. Spokane, WA.

- **Hansen, A. G.**, and C. J. Farrell. Are Walleye a boost or bane to Colorado fisheries? A continental division. 152nd Meeting of the American Fisheries Society. August 22, 2022. Spokane, WA.

- Jackson, K. N., C. J. Farrell, B. M. Johnson, C. A. Myrick, **A. G. Hansen**, and Y. Kanno. Prey selection of diploid and triploid Walleye in a prey-limited system. Colorado State University Celebrate Undergraduate Research and Creativity Showcase. April 21, 2022. Fort Collins, CO.

Internal Presentations:

- Farrell, C. J., B. M. Johnson, **A. G. Hansen**, C. A. Myrick, M. M. Brandt, and J White**.** Results from the CPW-CSU triploid Walleye project. Northeast Region Biology Days. April 28, 2022.

- **Hansen, A. G.** Assessment of Walleye broodstocks in Chatfield, Cherry Creek and Pueblo reservoirs. Northeast Region Biology Days. April 28th, 2022.

- **Hansen, A. G.**, and J. M. Lepak. The dynamic history of Walleye and their forage base—Rainbow Smelt—in Horsetooth Reservoir. Northeast Region Biology Days. April 28th, 2022.

- **Hansen, A. G.**, and C. Tucker. Integrating angler dynamics and Walleye biology to explore alternative harvest strategies for broodstock in Pueblo Reservoir. Southeast Region Conservation Days. May 11th, 2022.

Other Research Communication & **Technical Assistance:**

- Anonymous peer reviewer for: Environmental Pollution (1 manuscript); Fishes (1 manuscript); NeoBiota (1 manuscript);

- Advised CPW staff on collection of paired blood and fin clip tissue from putative triploid Colorado River Cutthroat Trout and corresponded with the Eagle Fish Genetics Laboratory in Idaho to develop molecular approach to ploidy determination.

- Reviewed Utah Division of Wildlife Resources modeling report of appropriate triploid Walleye stocking procedures for the U.S. Fish and Wildlife Service and the Upper Colorado River Basin Endangered Fish Recovery Program.