Lake and Reservoir Research

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

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LAKE AND RESERVOIR RESEARCH

Period covered: December 2023 – November 2024.

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:	Mysis diluviana investigations: An evaluation				
	Legumine CFT (5% active rotenone) toxicity.				

OBJECTIVES

Evaluate the susceptibility of invasive *Mysis diluviana* to varying concentrations (0.4, 46.0, 83.0, 160.0, 384.5, 1472.5, and 3248.4 ppb) of Legumine CFT (5% active rotenone) at 24, 48, 96, and 192-hours.

MANUSCRIPT

Lepak, J. M., W. M. Pate, P. Cadmus, A. G. Hansen, K. D. Gallaher, D. B. Silver. 2024. Response of an invasive aquatic crustacean to the fish toxicant rotenone. Lake and Reservoir Management. 40(3):330-337.

BACKGROUND

Fisheries managers have used the piscicide rotenone for decades in aquatic systems to control or eradicate fish species for a variety of purposes including nonnative species control and native fish conservation and restoration efforts (McClay 2000, 2005; Finlayson et al. 2018). Throughout northern North America *Mysis diluviana* (opossum shrimp; formerly known as *M. relicta*) were introduced primarily to improve foraging opportunities for sport fish. However, widespread introductions proved harmful, creating competitive conditions between introduced *M. diluviana* and salmon and trout for cladocerans and other food resources (Lasenby et al. 1986; Martinez and Bergersen 1991). Thus, managers have sought to minimize the impact of *M. diluviana* where their introduction reduced zooplankton densities and salmonid growth (Martinez and Bergersen

1989). Here, we evaluate the median 50% lethal concentrations (LC50s) for *M. diluviana* at 24, 48, 96, and 192 h using active rotenone concentrations within, and exceeding recommended application limits (0–4111 ppb) to determine the potential effects of rotenone exposure on *M. diluviana*.

MANUSCRIPT ABSTRACT

Fisheries managers have used the piscicide rotenone to achieve a variety of management objectives for decades in aquatic systems, yet the effects of rotenone on many species are not well understood. We tested the effects of rotenone on invasive *Mysis diluviana* that have deleterious effects on aquatic food webs (e.g., zooplankton communities) and ultimately some native and sport fishes. The 50% median lethal concentration (LC50) was determined for *M. diluviana* at 24, 48, 96, and 192-hours using active rotenone concentrations from 0 to 3,200 ppb. LC50s were not achieved at 24 and 48-hours, and at 96 and 192-hours, LC50s were estimated at 9,989 (95% CI = 3,601-16,378) and 607 (350-863) ppb, respectively, well above (50-fold and 3-fold) recommended rotenone application concentrations. These results suggest that rotenone concentrations and exposure times for effectively controlling *M. diluviana* will exceed allowable application limits, and likely harm more vulnerable non-target species disproportionately relative to *M. diluviana*. Future work should focus on compounds other than rotenone for evaluation, or alternative control methods that take advantage of potential vulnerabilities of *M. diluviana* (e.g., temperature sensitivity).



Figure 1. Rotenone dose-responses of *M. diluviana*. Estimated probabilities of mortality (solid lines) for *M. diluviana* at 96 and 192-hours are provided as a function of rotenone concentration (ppb). Points are observed data and overlapping points have corresponding darker shading. Each treatment began with eight, live individuals, and responses were evaluated using mean rotenone concentrations of 0.4, 46.0, 83.0, 160.0, 384.5, 1472.5, and 3248.4. Dashed lines represent 95% confidence regions.

REFERENCES

Finlayson, B., R. Schnick, D. Skaar, J. Anderson, L. Demong, D. Duffield, W. Horton, and J. Steinkjer. 2018. Planning and standard operating procedures for the use of rotenone in fish management – rotenone SOP manual, 2nd edition. Bethesda: American Fisheries Society; [cited 15 Nov 2023]. Available from: https://units.fisheries.org/rotenone-stewardship/sop-manual/rotenone-sop-manual-2nd.

Lasenby, D. C., T. G. Northcote, and M. F. Fürst. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Canadian Journal of Fisheries and Aquatic Sciences. 43:1277-1284.

Martinez, P.J., and E. P. Bergersen. 1989. Proposed biological management of *Mysis relicta* in Colorado lakes and reservoirs. North American Journal of Fisheries Management. 9:1-11.

Martinez, P. J., and E. P. Bergersen. 1991. Interactions of zooplankton, *Mysis relicta* and kokanees in Lake Granby, Colorado. American Fisheries Society Symposium. In: Nesler TP, Bergersen EP, editors. Mysids in fisheries: hard lessons from headlong introductions. Bethesda (MD): American Fisheries Society Symposium. 9:49-64.

McClay W. 2000. Rotenone use in North America (1988-1997). Fisheries. 20:15-21.

McClay W. 2005. Rotenone use in North America (1998-2002). Fisheries. 30:29-31.

<u>RESEARCH PRIORITY</u>:

Summer Profundal Index Netting (SPIN) for monitoring Lake Trout *Salvelinus namaycush*: Results from 2024 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 in lakes and reservoirs (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), Lake Granby (2014), Ruedi Reservoir (2023), and Taylor Park Reservoir (2013). Results from the 2024 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 July 22-24, 2024 wherein 79 nets were set, capturing a total of 229 Lake Trout ranging in size from 162 mm to 914 mm total length (TL; mean = 447 mm \pm 112 mm SD). Of the Lake Trout encountered, 68% ranged between 275 and 450 mm TL. Lake Trout were most prevalent in 30-40 m depths. The depth distribution, size structure, and extent of the catch in 2024 at the corresponding water surface elevation of Blue Mesa Reservoir produced a total Lake Trout abundance estimate of 23,573 fish \geq 162 mm TL (lower 68% confidence limit = 18,282; upper limit = 29,528). The catch of Lake Trout <275 mm TL was incidental (0.87%). Therefore, this abundance estimate best reflects fish \geq 275 mm TL (Table 1). The 2024 SPIN estimate was nearly double that of the 2022 estimate, demonstrating the ability of Lake Trout in Blue Mesa Reservoir to rebound quickly from angler harvest.

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 \geq 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
	Tuylor Turk	50	271				19101	010	11,000	,,,,,,,	1 1,5 11
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											
2016			100	120		1.47		2 400	24.260	16 530	20.040
	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											
2020	Bhe Meca	90	212	441	02	1.51	7 32	2 247	16 443	12 518	20.842
	Blue Wiesa	90	212	171	92	1.51	1.52	2,277	10,445	12,510	20,042
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	-		10.0								
2024	Rued1*	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

REFERENCES

Hansen, A. G. 2016. Summer profundal index netting for tracking trends in the abundance of Lake Trout in coldwater lakes and reservoirs of Colorado: results from 2016. Internal CPW report. 6 pages.

Lepak, J. M. 2011. Evaluating summer profundal index netting (SPIN) as a standardized quantitative method for assessing Lake Trout populations. Internal CPW report. 10 pages.

Lepak, J. M. 2013. Summer profundal index netting (SPIN) for Lake Trout population estimates in Grand Lake and Taylor Park Reservoir. Internal CPW report. 4 pages.

Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy Lake Trout in a montane reservoir. North American Journal of Fisheries Management 34:908-922.

Sandstrom, S., and N. Lester 2009. Manual of instructions for summer profundal index netting (SPIN): a Lake Trout assessment tool. Ontario Ministry of Natural Resources. Peterborough, Ontario. Version 2009.1. 22 pages + appendices.

RESEARCH PRIORITY:

Evaluating reservoir reoperation: Blue Mesa Lake Trout population expansion.

OBJECTIVES

Environmental flow management is a growing driver of dam reoperation in which impounded water is allocated to rivers for ecosystem benefits. Neglected however, are the upstream effects of reoperation on reservoir ecosystems, despite their global importance in providing critical social-ecological services such as supporting inland fisheries and contributing to water and food security. Here, we compiled fisheries survey data spanning five decades to evaluate responses to the environmental flow-driven reoperation of a large montane reservoir in the arid southwestern United States. Modeling indicated that following reoperation, predator population productivity increased 11-fold. Collectively, results lend evidence that reoperation can disrupt upstream ecosystem services and necessitate adaptation by management systems to mitigate. These outcomes highlight the broader importance of considering ecological integrity and sustainability both upstream and downstream in the context of dam reoperation. More comprehensive understanding of the reciprocal effects of 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 social-ecological contexts.

MANUSCRIPT SUBMISSION

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FULL MANUSCRIPT

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5	Not just water over the dam: upstream ecosystem disruption following
6	reoperation for environmental flows
7	
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18 Abstract

Environmental flow management is a growing driver of dam reoperation in which 19 impounded water is allocated to rivers for ecosystem benefits. Neglected, however, are the 20 upstream effects of reoperation on reservoir ecosystems, despite their global importance in 21 providing critical social-ecological services such as supporting inland fisheries and contributing 22 to water and food security. Ecologists have long devoted effort to understanding functional 23 relationships among river flows, habitat, and species life history to inform conservation actions. 24 Complimentary efforts linking water use patterns to reservoir ecology are disproportionately 25 26 rare, limiting 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 27 responses to the environmental flow-driven reoperation of a large montane reservoir in the arid 28 southwestern United States. Reoperation reduced late-season reservoir drawdowns by 74% (13.6 29 m to 3.5 m on average), which coincided with the population expansion of an introduced apex 30 predator and subsequent destabilization of a fishery worth millions to local and regional 31 economies. The degree of late-season water level stabilization was sufficient to facilitate 32 predator reproduction based on life history and spawning behavior. An exponential growth 33 34 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 the survey 35 data and predator expansion. Modeling indicated that following reoperation, predator population 36 37 productivity increased 11-fold. Collectively, results lend evidence that reoperation can disrupt upstream ecosystem services and necessitate adaptation by management systems to mitigate. 38 39 These outcomes highlight the broader importance of considering ecological integrity and 40 sustainability both upstream and downstream in the context of dam reoperation. Further,

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widespread reoperation is anticipated to hedge against climate change, human population
growth, and other factors, and may not be conservation driven. The context of reoperation will
also be regionally and situationally dependent wherein conservation concerns upstream could
conceivably outweigh those downstream. More comprehensive understanding of the reciprocal
effects of 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 socialecological contexts.

- 48
- 49 **KEYWORDS**: apex predator, population expansion, reproductive success, reservoir food web,
- 50 river regulation, water level fluctuations

51 INTRODUCTION

Dams are prominent fixtures on our landscapes (Nilsson et al., 2005; Poff et al., 2007). 52 These infrastructures have altered flow regimes and disrupted ecological processes important for 53 maintaining native biodiversity and ecosystem function in rivers worldwide (Poff et al., 1997; 54 Reid et al., 2019). Dam removal is a growing practice or consideration for restoring the 55 ecological integrity of rivers (Brown et al., 2024; O'Connor et al., 2015; Schiermeier, 2018). 56 Environmental flow management offers another approach when dam removal is not possible and 57 is regarded as a critical action to curb global freshwater biodiversity loss (Tickner et al., 2020). 58 59 With this strategy, impounded water is allocated to rivers for ecosystem benefits (Baruch et al., 2024) and may be designed to capture key functional elements of natural flow and temperature 60 regimes (Yarnell et al., 2015) or balance trade-offs between environmental and societal needs 61 (Bestgen et al., 2020; Chen & Olden, 2017). 62

Managing for environmental flows requires dams to be reoperated in which traditional 63 water storage and release patterns are modified to achieve new downstream objectives, but not 64 without challenges (Horne et al., 2017; Opperman et al., 2019; Richter & Thomas, 2007). 65 Neglected, however, are the upstream effects of reoperation. Reservoir ecosystems are 66 increasingly recognized for their global importance in providing critical social-ecological 67 services. These include water security and provisioning, which are vital in arid/semi-arid regions 68 (Turley et al., 2022), and the inland fisheries they support make essential contributions to food 69 70 security/systems and economies (Lynch et al., 2016; Lynch et al., 2024; Parisek et al., 2024). Deep oligo/mesotrophic reservoirs offer coldwater refuge habitats increasingly needed for 71 conserving coldwater specialist species (Hansen et al., 2022; Kovach et al., 2017). Because 72 73 impoundments are permanent fixtures in many regions and provide critical services (Chen &

Olden, 2017), it is prudent to consider ecological integrity and sustainability on both sides ofdams in the context of reoperation.

Ecologists have long devoted efforts to understanding relationships among river flows, 76 habitat, species life history requirements, and ecosystem functionality to predict responses to 77 change and inform conservation actions (Baruch et al., 2024; Lytle & Poff, 2004; Mims & 78 Olden, 2012; Yarnell et al., 2015). Complimentary efforts linking dam operations and resulting 79 water use patterns to ecological processes within reservoirs (e.g., Saito et al., 2001) are 80 disproportionately rare, limiting our ability to predict responses and conduct more inclusive 81 82 assessments of the multi-use tradeoffs associated with reoperation (e.g., Chen & Olden, 2017). Further, we are aware of no explicit studies evaluating how environmental-flow-driven 83 reoperation affects upstream reservoir ecosystems, with an emphasis on services provided by 84 food webs and fisheries. Indeed, traditional operations and water use can affect reservoir trophic 85 ecology (Eloranta et al., 2016; Hansen et al., 2022), food web structure (Hansen et al., 2018; 86 Murphy et al., 2019a), benthic communities (Evtimova et al., 2016), and the reproductive 87 success of fishes (Felts et al., 2020; Gaboury & Patalas, 1984; Kahl et al., 2008), but how these 88 effects mediate species interactions over longer time scales is poorly understood. 89 90 Dam reoperations and flow manipulations, in essence, represent large-scale natural

experiments. Such events provide important opportunities to assess ecological responses at
relevant scales (Barley & Meeuwig, 2017; Schindler, 2012). Similar to assessing environmental
flow responses (Baruch et al., 2024; Olden et al., 2014), long-term studies with monitoring
before and after reoperation are needed to effectively evaluate upstream effects. In this study, we
compiled fisheries survey data spanning five decades to evaluate responses to the environmentalflow-driven reoperation of a large montane reservoir in the arid southwestern United States.

97 Here, reoperation modified the stability of late-season water levels, which coincided with the population expansion of an introduced apex predator. Expansion had rippling effects that 98 destabilized a predator-prey system and socially-valued recreational fishery worth millions 99 (USD) to local and regional economies and now requires ongoing management 100 intervention/adaptation. Specifically, we apply established principles of invasion ecology to 101 develop an exponential growth modeling framework integrating survey data to examine evidence 102 for the hypothesis that reoperation and corresponding modifications to late-season reservoir 103 water levels promoted predator expansion through improved reproductive success. 104

105 METHODS

106 System and fishery

Blue Mesa Reservoir is a 3,793 ha mesotrophic impoundment on the Gunnison River in 107 southwestern Colorado, USA (Figure 1A). The earthen dam was completed in 1965. Filling 108 finished in 1970. Reoperation occurred in 1993 to improve downstream flow conditions for 109 endangered fishes endemic to the Colorado River and its tributaries (Tyus, 1992). Traditional 110 operations emphasized stable releases for hydropower generation and drawing down the 111 reservoir over fall and winter to capture spring snowmelt. The goal of reoperation was to 112 113 generate an annual peak flow pulse in spring (contingent on inflows and in-reservoir storage targets; Johnson et al., 2004), an important functional element of regional snowmelt-driven 114 hydrographs (Van Steeter & Pitlick, 1998). As a result, the seasonal pattern of water releases 115 116 inverted (Johnson & Koski, 2005). After reoperation, relative releases were generally lower during fall and winter and higher during spring versus traditional operations (Figure 1B). 117 118 Blue Mesa Reservoir supports a recreational fishery for introduced salmonids, including kokanee salmon (Oncorhynchus nerka), rainbow trout (O. mykiss), brown trout (Salmo trutta), 119

12

120	and lake trout (Salvelinus namaycush). Regional fisheries managers emphasize salmonids given
121	their limited effects on native fishes if entrained downstream (Hansen et al., 2019). The fishery
122	was valued at >5 million USD annually by Johnson & Walsh (1987) and has attracted
123	participants from 49 US states (Johnson & Koski, 2005). The reservoir serves as a primary wild
124	broodstock for kokanee (exhibit limited natural reproduction), which supports stocking and
125	kokanee fishing across Colorado valued at 29 million USD annually (Johnson & Butteris, 2009).
126	Lake trout fingerlings were stocked inadvertently in 1968 (28,000; Wiltzius, 1974), then
127	purposefully in 1972-1974 (18,060-35,200), 1988 (10,000), and 1992 (24,709). Annual stocking
128	of kokanee fingerlings started in 1966. When abundant, kokanee attract >50% of anglers and
129	dominate open water catch and harvest (>80%; Johnson & Koski, 2005). Angler catch rates of
130	kokanee are tightly coupled to kokanee abundance/density, which is positively related to fishing
131	effort (Johnson & Martinez, 2000). Kokanee also support rapid growth rates in their predators
132	(Johnson et al., 2017b), and lake trout can exceed a meter in length and 22 kg (Johnson &
133	Martinez, 2000; Martinez et al., 2009). For these reasons, sustaining a kokanee fishery by
134	stocking has been the primary management objective since impoundment.
135	Evidence for strong or consistent natural reproduction by lake trout was not observed
136	until the mid-1990s; indicated by the stable presence and increasing catch rate of sub-adults in
137	the angler creel despite declining fishing effort (Figure 2A; Pate et al., 2014). Although stocking

in 1988 and 1992 may have influenced short-term catch rates, catches, harvests and size-

structure expanded through the 2000s after stocked fish surpassed the size (330-550 mm) and age

140 (age-3 to 6) most vulnerable to anglers (Figure 2B; Hansen, 2018). Conversely, catch rates

increased after stocking in 1968 (first caught in 1971; Wiltzius, 1978), but diminished by the

142 early 1980s (Van Buren & Burkhard, 1981) and remained low given minimal representation in

143 the 1989 creel, prompting additional stocking (Figure 2A). Johnson & Walsh (1987) noted low summer catches of lake trout in 1986. Female lake trout in Blue Mesa Reservoir mature at 144 measurable rates around age-4 ($\sim 20\%$) and reach 50% maturity around age-6. From these 145 timelines, detectable reproduction was possible over a decade before the mid-1990s. 146 Unsustainable predation on kokanee by expanding lake trout deteriorated the fishery 147 during the 2000s (Figure 2C) despite progressively relaxing lake trout harvest regulations 148 (Johnson & Martinez, 2000) and maximizing hatchery capacity by over-doubling the annual 149 stocking rate of kokanee (Figure 2D). Kokanee collapsed in 2009 (>90% reduction in peak 150 151 abundance; Figure 2C), kokanee harvest declined by >80% (Figure 2D), and the body condition of lake trout diminished, degrading the trophy component (Figure 2E). Kokanee egg collections 152 at the upstream hatchery became more variable (Figure 2F). Agency-sponsored fall gill netting to 153 remove and control lake trout and liberalization of lake trout harvest began in 2009. Control 154 efforts generally targeted smaller lake trout that exhibited the greatest population-level predation 155 pressure on kokanee to maintain coexistence with the trophy fishery (Pate et al., 2014). The daily 156 bag limit for kokanee was reduced from ten to five fish in 2011. Increased kokanee abundances 157 and lake trout body conditions were observed one decade after removals and other actions 158 159 started. Removal of lake trout was postponed in 2018 and replaced by providing harvest incentives to anglers in 2020 (Hansen et al., 2021). 160

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Fisheries-dependent survey data

Estimates of lake trout catch rate and harvest by anglers were compiled from historic agency reports (Table S1, Supporting Information). Federal agency personnel counted boat and shore anglers at access points and across the reservoir twice daily every month of the year prior to 1980 (1971-1977). Counts ($\widehat{ANG}_{total,t}$) were considered a census (Wiltzius, 1974). Counts were paired with catch and effort data from boat and shore anglers (that had completed trips) interviewed January-October independently by state agency personnel to estimate a grand mean retained catch-per-angler-hour ($C_{ret}PAH_t$; fish/1,000 fishing h) and a grand mean daily trip duration (\widehat{DUR}_t ; h) for each year t. Mean annual harvest ($\widehat{H}_{A,t,i}$) was estimated by:

170 (1)
$$\hat{H}_{A,t,i} = C_{ret} P \bar{A} H_t \times \bar{D} U \bar{R}_t \times \bar{A} N \bar{G}_{total,t} \times \hat{p}_{t,i}$$

171 where $\hat{p}_{t,i}$ was the grand mean proportion of species *i* in the catch (Wiltzius, 1978).

For 1971-1977, Van Buren & Burkhard (1981) noted a systematic bias in the estimation 172 of $\hat{p}_{t,i}$ toward fishes more accessible to shore anglers (rainbow and brown trout) versus pelagic 173 fishes (lake trout and kokanee) given the propensity for clerks to interview shore over boat 174 anglers. As a result, rainbow and brown trout erroneously dominated catch compositions 175 (upwards of 98-99% in some years) and lake trout were reported at trace levels ($\leq 0.01\%$; 176 Wiltzius, 1974, 1978). Early surveys were reexamined in 1978-1979 using a new statistical 177 computing approach (Nuhold & Lu, 1957; Powell, 1980), which indicated an under-178 179 representation of pelagic fishes by a factor of 5-15 (Van Buren & Burkhard, 1981). Therefore, we adjusted values of $C_{ret}PAH_t$ assuming an average $\hat{p}_{t,i} = 1.0\%$ (~10-fold higher than reported) 180 for lake trout. We also adjusted by the proportion of effort occurring May-October to align with 181 standard, pre-creeled catch rates (CPAH_{STND,t,i}; number/1,000 fishing h) estimated in 1980 and 182 later (see below). Because retention rates of nearshore fishes were high (>93%; Van Buren & 183 Burkhard, 1981), $C_{ret}PAH_{t,i}$ values reflected pre-creeled catch rates, so we assumed the adjusted 184 values for lake trout were comparable to $\widehat{CPAH}_{STND,t,i}$. Standard harvests $(\widehat{H}_{STND,t,i})$ were 185 estimated by multiplying reported $\hat{H}_{A,t,i}$ values by 1.0% for the proportion lake trout in the catch, 186

effort within May-October, and by 0.25 to reflect differences in the daily bag limit for lake trout(1 daily) versus nearshore fishes (4 daily).

Surveys in 1980 and later (Van Buren & Burkhard, 1981; Johnson & Walsh, 1987; 189 present study) used a stratified-random design to estimate grand mean $\widehat{CPAH}_{STND,t,i}$ and $\widehat{H}_{STND,t,i}$ 190 within/over the standard May-October open water fishing season (1980, 1982, 1989, 1993-2012) 191 and the January-April winter and ice-off season ($\widehat{CPAH}_{w,t,i}$ and $\widehat{H}_{w,t,i}$; 1984, 1986, 2004, 2006, 192 2012). Strata included reservoir basin and weekday or weekend. Counts of boat, shore or ice 193 anglers occurred at 2-3 designated times on randomly selected days each week. Paired interviews 194 were proportional to counts by angler type. Angler use during November-December was often 195 negligible as poor weather or ice conditions limited anglers. Thus, $\hat{H}_{STND,t,i} + \hat{H}_{w,t,i}$ from latter 196 surveys equated to $\hat{H}_{A,t,i}$ from early surveys in years when both periods were evaluated. 197 Consistent over time was consultation with and software development by David Bowden 198 (Colorado State University), which helped ensure continuity among estimates (Wiltzius, 1978; 199 Powell, 1980; Schisler & Bowden, 2012). 200

201

Fisheries-independent survey data

The abundance (\hat{N}) of catchable lake trout was estimated in 2002, 2011, 2014, 2016, and 2018 (Table S1, Supporting Information). In 2002, mark-recapture data integrated over 2000-2020 were used to estimate the \hat{N} of piscivorous-sized lake trout \geq 425 mm total length (TL; 2020 Crockett et al., 2006). A candidate set of Cormack-Jolly-Seber models with alternative 2021 hypothesized effects of different variables (e.g., time and TL) on apparent survival (ϕ) and 2027 capture probability (*P*) were compared using Akaike's information criterion utilizing second-2038 order approximations (AIC_c; Burnham & Anderson, 1998). Models with Δ AIC_c <2.0 were averaged by AIC_c weight to obtain final parameter estimates, and \hat{N} was a derived parameter.

210 We increased \hat{N} by the relative frequency of lake trout <425 mm TL captured in the 2002 creel 211 to align this estimate with the full length-range vulnerable to anglers.

Abundance estimates after 2002 were obtained using Summer Profundal Index Netting 212 (SPIN; Sandstrom & Lester, 2009). Briefly, SPIN is a stratified-random gill netting protocol in 213 214 which experimental benthic gill nets are set during thermal stratification for short durations (2 h \pm 20 min) within defined depth-strata spanning 10-80 m at randomized locations across the 215 reservoir (81-95 individual sets annually). Effort was proportioned by reservoir basin and depth-216 strata surface area and weighted by depth-specific catch rates of lake trout progressively over the 217 218 surveys. The sizes of lake trout vulnerable to SPIN aligned with those catchable by anglers. The protocol accounted for year-to-year changes in reservoir surface elevation. 219

220 The density of catchable lake trout (\hat{D} ; number/ha) was estimated by first computing size-221 selectivity adjusted catch-per-unit-effort in each depth stratum h ($\widehat{CPUE}_{sel,h}$):

222 (2)
$$\widehat{CPUE}_{sel,h} = \sum_{m=1}^{m=n_h} \frac{1}{s_{m,h}} / sets_h$$

where s_m is the gill net selectivity coefficient for lake trout *m*, which is a function of lake trout fork length ($s_m = f(FL_m)$; provided in Sandstrom & Lester, 2009), n_h is the total number of lake trout captured within *h*, and *sets_h* is the total number of gill nets set within *h*. These values were weighted by depth-strata surface area and multiplied by the "large-bodied" population correction factor (4.86; forage base supported by fish; Sandstrom & Lester, 2009) to obtain \hat{D} :

228 (3)
$$\widehat{D} = \sum_{h} p_h \times \widehat{CPUE}_{sel,h} \times 4.86$$

where p_h is the proportion of stratum h of total area surveyed (ha >10 m deep). Estimates of \widehat{D} 229 were expanded to \hat{N} based on area surveyed. Close alignment between SPIN and an independent 230 mark-recapture study in a separate Colorado lake (Lepak, 2013), and alignment of mark-231 232 recapture and SPIN estimates to expanding angler catch rates through the 2000s/2010s in Blue 233 Mesa Reservoir, corroborated this approach (Pate et al., 2014), as well as the joint use of 234 fisheries-dependent and independent data.

235

Linking dam operations to lake trout life history

Lake trout spawn in fall in water depths and habitats that can vary. However, lake trout 236 are most often reported spawning along shallow rocky shoals or shorelines less than ~12 m deep 237 238 where wind and wave action keeps interstitial spaces clean of sediments (Cox, 2010; Gunn, 1995; Scott & Crossman, 1973). Spawning at greater depths can occur (Dux et al., 2011), and 239 diversity in spawning behavior may increase with lake size (Bigelow, 2009). Deep-water 240 241 spawning may be advantageous for incubating eggs by limiting physical stressors that cause mortality or the abundance of egg predators (Fitzsimons et al., 2005), but presents biological 242 243 challenges (e.g., gas bladder inflation and limited forage) to emerged fry and may not be successful (Janssen et al., 2007). Despite the potential for diverse spawning behavior, lake trout 244 reproduction could be limited under some reservoir operational regimes. Specifically, those that 245 continuously release water over fall and winter for hydropower and to mitigate spring runoff (as 246 in Blue Mesa traditionally), as this could result in the total or partial dewatering or freezing of 247 shallow-water spawning areas over the egg incubation and alevin yolk-sac absorption periods 248 (Benoît & Legault, 2002). 249

For Blue Mesa Reservoir, we analyzed water surface elevations to determine whether the 250 magnitude of late-season drawdowns before and after reoperation could limit lake trout 251

18

reproductive success based on their spawning behavior. Data were freely available online fromthe US Bureau of Reclamation at:

254 https://www.usbr.gov/uc/water/hydrodata/reservoir data/site map.html (accessed October 26,

- 255 2024). First, we computed the mean monthly surface elevation (m) of the reservoir by year
- 256 (Figure 1C). For each year, we computed the magnitude of mean drawdown (or rise) from
- 257 October, when lake trout begin spawning, to the low (or high) point of winter or spring (April at
- the latest if continuous drawdown or rise) the following year (defined here as "fall-to-spring
- flux" [m]; Figure 1D). Lastly, a two-intercept, single change-point, regression model was applied
- using the "mcp" package in R (Lindeløv, 2023; R Core Team, 2023) to (1) test whether a
- biologically significant regime shift in the magnitude of late-season flux occurred following
- 262 reoperation, and (2) inform candidate model structures (see below).

263 Conceptual framework for modeling

Delays in the population or range expansion of introduced species and effects on 264 ecosystems are common (Crooks & Soule, 1999). Delays may be inherent, or expected based on 265 the early, slow period of exponential growth, a robust model of animal invasion dynamics. 266 Alternatively, delays may be longer than expected from exponential growth, indicating the 267 268 presence of, and ultimate release from, a limiting factor (Crooks, 2005). Aikio et al. (2010) refined these definitions to enable quantitative description and testing. If inherent, early 269 population dynamics should be explained by a one-stage process or mathematical expression 270 271 (e.g., single exponential function). Alternatively, if unexpected, a two-stage process (i.e., two separate functions) would be required. Therefore, a one-stage process represents a null 272 expectation grounded in invasion ecology, whereas any deviation requires additional biological 273 274 explanation (Aagaard & Lockwood, 2014). We apply these principles to our time-series of

275 fisheries survey data for lake trout in Blue Mesa Reservoir. Our null expectation was that the survey data could be described by a one-stage exponential growth model, meaning the expansion 276 of lake trout occurred independently of dam reoperation or other factors, and was driven by 277 factors inherent to their biology. Data support for a two-stage model would indicate significant 278 biological influence from an external factor, with our primary hypothesis being a regime shift in 279 dam operations that reduced late-season reservoir flux and enhanced lake trout reproduction. 280 Evidence for the latter was evaluated by relating observed dam operations to lake trout spawning 281 behavior. 282

Base exponential growth model

Exponential growth described expansions of introduced lake trout in other western North 284 American lakes (Ellis et al., 2011; Hansen et al., 2008; Ruzycki et al., 2003), so it was an 285 appropriate assumption for the process underpinning dynamics in Blue Mesa Reservoir. We 286 developed a deterministic exponential growth model that provided expected values for each 287 survey data observation/component compiled over the 1971-2018 period (\hat{N} [n = 5 observations]; 288 \widehat{CPAH}_{w} [n = 5]; \widehat{H}_{w} [n = 5]; \widehat{CPAH}_{STND} [n = 30]; \widehat{H}_{STND} [n = 30]) using trajectory matching 289 (Bolker, 2008). Expected starting abundance (N_{1971}) was defined by the first lake trout stocking 290 event (28,000 fingerlings in 1968) and appearance in creel (1971): 291

292 (4)
$$N_{1971} = 28,000 \times S_{0-3}$$

where S_{0-3} is the survival rate of stocked fish from age-0 to age-3 in spring when they recruit to the fishery. Next, the expected abundance (*N*) of catchable lake trout in year *t* was described as:

295 (5)
$$N_t = N_{t-1}(1+r) - H_{w,t-1} - H_{STND,t-1} - RM_{t-1} + Stocked_{age-3,t}$$

where *r* is the annual rate-of-change (reflects intrinsic population productivity), *RM* is the known number removed during fall gill netting (2009-2017), and *Stocked*_{age-3} is the expected number of age-3 fish recruiting to the catchable population based on the known number of age-0's stocked

299 3 years prior ($Stocked_{age-0}$):

300 (6)
$$Stocked_{age-3,t} = Stocked_{age-0,t-3} \times S_{0-3}$$

301 For all years, expected winter ice and ice-off harvests were computed as:

302 (7)
$$H_{w,t} = N_t \mu_w$$

303 and standard harvests as:

304 (8)
$$H_{STND,t} = (N_t - H_{w,t}) \mu_{STND}$$

305 where μ_w and μ_{STND} are exploitation rates. Expected angler catch rates were modeled

306 concomitantly with *N*. For winter and ice-off:

$$307 \quad (9) \qquad CPAH_{w,t} = N_t q_w$$

308 and for the standard period:

$$309 \quad (10) \qquad CPAH_{STND,t} = (N_t - H_{w,t})q_{STND}$$

where q_w and q_{STND} are catchability coefficients. Model parameters included S_{0-3} , r, μ_w , μ_{STND} , q_w , and q_{STND} .

312 Specification of one- and two-stage models

Parametrization of the base exponential growth model was modified to reflect one- and two-stage population growth. The one-stage process assumed a single *r* governed dynamics over the entire 1971-2018 period. The two-stage process assumed a regime shift in *r* linked to dam reoperation. In this model, dynamics were governed by two *r* parameters, one for traditional operations ("trad"; r_{trad} ; 1976-1990) and one for environmental flow operations ("ef"; r_{ef} ; 1991-2018). The year the regime shift occurred (1988; see Results) was informed by change point regression on the time series of fall-to-spring flux (Figure 1D). From this year, a three year offset was included to account for the delay in lake trout recruitment to the fishery and expected shift in population rate-of-change. For both the one- and two-stage models, regime-dependence was incorporated for exploitation (μ_{w-trad} , μ_{w-ef} , $\mu_{STND-trad}$, $\mu_{STND-ef}$) and catchability (q_{w-trad} , q_{w-ef} , q_{STND} t_{rad} , $q_{STND-ef}$) given notable differences in fisheries management between periods. Lake trout were protected by harvest regulations traditionally, but regulations were relaxed and harvest was

325 encouraged during population expansion.

326 Model fitting and comparison

Given the propensity for exponential growth to characterize the expansion process of introduced species, we only considered observation error. We assumed survey observations for each data component were lognormally distributed. The likelihood (*L*) of each survey observation from year *t* within data component *j* (denoted by \hat{X}) was:

331 (11)
$$L(\ln(\widehat{X}_{j,t})|\theta_{stage}) \sim N(\ln(X_{j,t}), \widehat{CV}_{j,t}^2)$$

where θ_{stage} is the set of parameters for either the one- or two-stage model, $X_{j,t}$ are model expected values corresponding to years with survey observations, and $\widehat{CV}_{j,t}$ are survey-derived coefficient of variation estimates used to approximate standard deviations within the likelihoods (Table S1, Supporting Information). Using survey-derived *CV*s in the likelihoods reflected a data weighting approach to clarify the mean population trajectory of lake trout.

Model parameters were estimated by minimizing the negative log-likelihood (NLL) summed across observations (n = 75) using the "mle2" function within the "bbmle" package (version 1.0.25; Bolker, 2022) in R (code provided in Supporting Information). Logit-link functions were used to keep stocking survival and exploitation rate parameters within their expected range of 0-1, and log-link functions were used to keep the catchability parameters 342 positive (Essington, 2021). We placed a minimum constraint on the model predicted abundance (1.0 fish) and CPAH (0.01 fish/1,000 h) of lake trout to avoid numerical errors (from negative or 343 zero values) within the lognormal likelihoods, which did not influence parameter estimates. We 344 used a combination of optimization approaches, beginning with a stochastic global algorithm 345 (Simulated Annealing; "SANN" in R) less susceptible to local minima, followed by a more local 346 algorithm (Nelder-Mead Simplex; Bolker, 2008). Best fit parameters were recovered from three 347 disparate starting positions to ensure model convergence. Approximate confidence intervals (CI; 348 95%) for parameter estimates were derived from likelihood profiles using the "confint" function 349 350 in R. Relative support for the one- and two-stage models was assessed using AICc (Burnham & Anderson, 1998). 351

352 **RESULTS**

353 Dam operations and lake trout life history

Change-point regression identified 1988 as the beginning of a new distinct regime in fall-354 to-spring flux, which preceded dam reoperation in 1993 by five years. This is likely because 355 minimal fluxes were observed from 1988-1990. During this period, inflows were reduced, and 356 the reservoir was recovering from failing to completely fill in 1988 (Figure 1C,D). Independent 357 of operational regime, minimal fluxes were generally observed during periods of low reservoir 358 elevation (driven by drought), as storage was retained to meet targets (Figure 1C,D). Before 359 1988, flux averaged 13.6 m (95% CI = 11.4-15.9 m) under traditional operations, but only 3.5 m 360 361 (2.0–5.2 m) after 1988 while predominately under operations for environmental flows (Figure 1D). Given the reported spawning behavior of lake trout (see above), these patterns supported the 362 notion that reproductive success in Blue Mesa Reservoir was more limited under traditional 363 364 operations than under operations for environmental flows.

365 Comparison of one- and two-stage models

We found the most support for the two-stage exponential growth model (n = 12) 366 parameters including year delineating regime shift; NLL = 156.28; AICc = 341.59; $\Delta AICc =$ 367 0.00) when compared to the one-stage model (n = 10 parameters; NLL = 172.81; AICc = 369.06; 368 $\Delta AICc = 27.49$). The difference in AICc values ($\Delta AICc$) between models was large enough to 369 370 consider the one-stage model unlikely (Burnham & Anderson, 2002), which was also evidenced visually by model fits (Figure 3). For creel survey estimates between 1971–1977, there was a 5-371 15 fold bias against pelagic oriented fishes like lake trout, so we assumed $\hat{p}_{t,i} = 1.0\%$ (reflecting a 372 mean 10-fold increase) to correct survey estimates in these years. Evidence for the two-stage 373 model was robust to this full range of bias. Assuming $\hat{p}_{t,i} = 0.5\%$ (5-fold bias), $\Delta AICc$ for the 374 one-stage model = 23.59, and 32.77 assuming $\hat{p}_{t,i} = 1.5\%$ (15-fold). Parameter estimates were 375 also similar across values considered for $\hat{p}_{t,i}$ (Table S6, Supporting Information). 376 377 Fit of the two-stage model and parameter estimates indicated that the lake trout fishery was supported predominately by stocked fish under traditional dam operations, then natural 378

origin fish under operations for environmental flows. The model demonstrated a large influx of 379 lake trout following early stocking, then a progressive decline to a low point in 1989 before 380 population expansion (Figure 3). The estimate for S_{0-3} was 0.108 (95% CI = 0.070-0.157). The 381 estimate for r_{trad} was 0.032 (-0.036–0.127), reflecting little to no population growth as stocked 382 fish numbers diminished (from exploitation or natural mortality), while the estimate for r_{ef} was 383 384 an order of magnitude higher (0.375; 0.309–0.481), reflecting population increase (Table 1). 385 Parameter estimates for exploitation rates and catchability coefficients from the two-stage model also aligned with expectations from regime-specific differences in harvest management. Values 386 387 for each parameter were higher under environmental flows-when regulations were

388 progressively relaxed and harvest was encouraged—than under traditional operations, and this 389 pattern was consistent between fishing seasons. These patterns were reversed for the one-stage 390 model during the standard creel period (Table 1).

391 **DISCUSSION**

Our assessment of dam operations and modeling framework provided evidence that 392 environmental flow-driven reoperation significantly disrupted upstream ecosystem services. 393 Reoperation stabilized late-season reservoir water levels. Modeling indicated that the intrinsic 394 population productivity of the reservoir's apex predator increased 11-fold following these 395 396 changes. This led to unsustainable predator-prey interactions and a series of reactionary modifications to the fisheries management system. Given the dual importance of environmental 397 flow management as a conservation action, and reservoir ecosystem services, this study 398 demonstrates the need for improved understanding of linkages between dam operations and 399 reservoir ecology to better predict responses to reoperation and adjust management preemptively. 400 We are not suggesting that upstream considerations should take precedence over downstream. 401 Rather, acknowledging that unintended effects to human-manipulated, but socio-economically 402 important, ecosystems upstream are possible, and more inclusive consideration of these effects is 403 404 warranted. Further, environmental flows are not the only driver of reoperation. Widespread adaptations are anticipated to hedge against climate change, human population growth, or other 405 factors (Dettinger et al., 2015; Ehsani et al., 2017; Miranda et al., 2020; Watts et al., 2011), so 406 407 applications will be diverse and not always conservation driven.

The exponential model accounted for exploitation and temporal changes in angler catchability when evaluating evidence for a two-stage population growth process, and covariates related to reservoir productivity, stocking practices, or egg production could not explain the 411 population expansion. An extensive review of water quality and trophic state indices based on total phosphorus, chlorophyll- α , and Secchi depth in 1999 (after the onset of expansion) 412 demonstrated that nutrient loading and mesotrophic conditions within the reservoir had not 413 changed over the preceding 25 years (Bauch & Malik, 2003; Johnson & Koski, 2005). Extensive 414 empirical food web and thermal modeling analyses conducted over 1993-2002 concluded that 415 operators had considerable latitude for modifying hypolimnetic water release patterns while 416 avoiding ecologically significant effects on reservoir thermal structure and productivity 417 (nutrients, phytoplankton and zooplankton) as already mediated by traditional operations 418 419 (Johnson et al., 2004; Johnson & Koski, 2005). The biomass of stocked salmonids (contributes to primary prey base) has remained relatively stable over the history of the fishery and exhibited a 420 declining per-capita trend with expanding lake trout. Coupling lake trout growth, maturation, and 421 fecundity (Pate et al., 2014) with cohorts stocked in known years and the mean population 422 trajectory, size-dependent increases in egg production could not compensate for declining lake 423 trout abundances preceding the 1990s and reproductive potential was likely relatively low at the 424 onset of expansion. 425

Assessing the life history characteristics of species in relation to reservoir morphometry 426 and existing or proposed reoperation strategies may inform predictions for potential upstream 427 effects on predator-prey productivity and interactions. Water level fluctuations on the scale of 428 meters to tens of meters can limit or enhance the reproductive success of fishes that spawn and 429 430 rear nearshore depending on how their direction, timing, and magnitude align with life history. For example, increasing or stable water levels during spring spawning improved the recruitment 431 of roach (*Rutilus rutilus*), whereas small drops ($\leq 1m$) following spawning caused complete year-432 433 class failure (Kahl et al., 2008). Overwinter drawdowns of 1-2 m reduced the year-class strength

434 of fall spawning lake whitefish (Coregonus clupeaformis) and cisco (C. artedii) (Gaboury & Patalas, 1984). Adfluvial fishes could be limited if drawdowns reduce physical access to 435 spawning tributaries (Hansen et al., 2022). Because lake community responses generally 436 manifest over a decadal time scale (Jeppesen et al., 2012), effects of reoperation may not be 437 immediately apparent. Preliminary evaluations however, could allow management systems to 438 439 adapt monitoring schemes to better detect potential responses and avoid ecological surprises. Hydrologic disturbance driven by human water manipulation and use also affects the 440 fundamental structure and function of lentic food webs (Evtimova & Donohue, 2016; Zohary & 441 442 Ostrovsky, 2011). For example, food web analysis of two analogous, impounded natural lake systems experiencing varying degrees of water use intensity (for irrigation) showed large 443 differences in trophic diversity. Trophic diversity in the system experiencing more extensive, 444 rapid, and early (spring/summer) versus late-season (late-summer/fall) drawdown was 445 compressed by 46% relative to the other. Compression occurred over the primary productivity 446 axis directionally toward pelagic-derived carbon and away from benthic-derived carbon, 447 indicating erosion of basal diversity fueling upper trophic level consumers (Hansen et al., 2018). 448 These patterns demonstrated the potential for water use during the primary growing season to 449 mute opportunity for benthic-pelagic coupling and benefits to system productivity, stability, and 450 adaptive capacity (McMeans et al., 2016). 451

452 Studies of food web structure, trophic interactions, and productivity in reservoirs or 453 impounded lakes reflect the often decades-long legacy of hydrologic disturbance (Eloranta et al., 454 2016; Hansen et al., 2022). However, because water use affects basal food web components and 455 the recruitment dynamics of fishes, ecological responses to departures from a dam's historic 456 function could still be complex and difficult to predict if reoperation results in notable changes to 457 seasonal water levels; particularly considering ongoing environmental change and the expected longer, more intensive periods of thermal stratification and drought (Dai, 2013; Tunney et al., 458 2014). While modeling and empirical assessment demonstrated negligible effects of reoperation 459 on the thermal structure and basal productivity of our study system (Johnson et al., 2004; 460 Johnson & Koski, 2005), ecologically-significant alterations are possible depending on dam 461 configuration (e.g., penstock elevation) or if water is withdrawn from thermal layers other than 462 the hypolimnion (Saito et al., 2001). Further, complex responses may be pronounced in systems 463 supporting diverse food webs or greater habitat complexity, owing to the synergistic effects of 464 465 warming, nutrients, and water use on surface level fluctuations, primary productivity, oxythermal habitat, and interactions with the life history, behavior, and thermal biology of native or 466 introduced species (Ellis et al., 2011; Jeppesen et al., 2010, 2012; Rolls et al., 2017). In simple or 467 subsidized (through stocking) food webs of low to intermediate productivity dominated by 468 pelagic-oriented species (our study system), predators can be tightly coupled to their preferred 469 prey (Johnson et al., 2017a; Schoen et al., 2012; Warnock et al., 2022). Although dynamic, 470 forecasting how these simpler interactions might respond to reoperation or other factors and 471 472 consequences for fisheries may be more tractable.

The social-ecological context underpinning dam reoperation and tradeoffs among conservation needs, recreational fisheries, and water provisioning or other factors is regionally and situationally dependent, and may be more multidimensional than demonstrated by our study system. For example, reservoirs and impounded lakes can be strong-holds for threatened species that exhibit high degrees of life history variation and inhabit both lotic and lentic environments (e.g., Kovach et al., 2017). Lentic environments can provide high foraging opportunity that support large-bodied, highly fecund, migratory individuals that may help populations persist and 480 resist invasive species (Dunham et al., 2008; Nelson et al., 2002). Thus, conservation concerns may be upstream of dams, while societal needs (e.g., water delivery for irrigation) may take 481 precedence downstream. In these situations, reoperation for more intensive water use may be 482 required to maintain downstream services in the face of environmental change and growing 483 burden on freshwater (Dai, 2013; Vorosmarty et al., 2000). Counter to our study, the challenge 484 here is not compromising lake or reservoir conditions (e.g., trophic interactions) that promote 485 native species productivity and persistence upstream (e.g., Hansen et al., 2022). Further, extreme 486 reoperation could convey benefits downstream and upstream. For example, drawdown of 487 488 reservoirs to their original streambed facilitated the outmigration of native anadromous salmon smolts while conferring survival benefits to future cohorts by disadvantaging invasive predators 489 remaining in the reservoir without compromising societal requirements for winter flood control 490 (Murphy et al., 2019a,b). Social-ecological contexts of reoperation will clearly be nuanced and 491 diverse and cannot be fully reviewed here. For most situations, however, explicit consideration 492 of potential reciprocal effects of reoperation and development of suitable monitoring programs 493 could be beneficial. 494

Reservoirs and impounded lakes are important infrastructures that provide critical social-495 496 ecological services such as flood control, water security and provisioning in many regions. They can also support valuable food and recreational fisheries comprised of native or introduced fishes 497 important for local and regional economies, and provide refuge habitats with high foraging 498 499 opportunity for species of conservation concern. To complement our understanding of river flow ecology, advancing our knowledge of how human water manipulation and use affects the 500 ecology of reservoirs and impounded lakes and cascading effects on food webs and fisheries or 501 502 other ecosystem services over relevant time scales is needed for better examination of tradeoffs

503	among expected downstream	and upstream	responses t	to reoperation	for environme	ental flows or
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- others drivers. More inclusive understanding of functional relationships may improve our ability
- to manage impoundments to better meet/maintain multiple objectives related to conservation-,
- 506 fisheries, and societal needs while adapting to climate change across a broad spectrum of social-
- 507 ecological contexts.

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- 512

513 DATA AVAILABILITY STATEMENT

- 514
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532 CONFLICT OF INTEREST STATEMENT

- 533534 The authors declare that there are no competing interests.
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- 539 **REFERENCES**
- 540
- Aagaard, K., and J. Lockwood. 2014. "Exotic Birds Show Lags in Population Growth." *Diversity and Distributions* 20: 547–554.
- 543
- Aikio, S., D. P. Duncan, and P. E. Hulme. 2010. "Lag-Phases in Alien Plant Invasions: Separating the Facts from the Artefacts." *Oikes* 110: 370–378
- Separating the Facts from the Artefacts." *Oikos* 119: 370–378.
- 547 Barley, S. C., and J. J. Meeuwig. 2017. "The Power and Pitfalls of Large-Scale, Unreplicated
- 548 Natural Experiments." *Ecosystems* 20: 331–339.
- 549
- Baruch, E. M., S. M. Yarnell, T. E. Grantham, J. R. Ayers, A. L. Rypel, and R. A. Lusardi. 2024.
 "Mimicking Functional Elements of the Natural Flow Regime Promotes Native Fish Recovery in
 a Regulated River." *Ecological Applications* 34: e3013.
- 553
- Bauch, N. J., and M. Malick. 2003. *Limnology of Blue Mesa, Morrow Point, and Crystal*
- 555 Reservoirs, Curecanti National Recreation Area, during 1999, and a 25-Year Retrospective of
- 556 Nutrient Conditions in Blue Mesa Reservoir, Colorado. Water Resources Investigations Report
- 557 02-4199, U.S. Geological Survey National Water Quality Assessment Program, Denver,558 Colorado.
- 559
- Benoît, J., and Legault, M. 2002. "Assessment of the Feasibility of Preventing Reproduction of
 Lake Charr, *Salvelinus namaycush*, in Shallow Areas of Reservoirs Affected by Drawdowns."
- 562 Environmental Biology of Fishes 64: 303–311.
- 563
 564 Bestgen, K. R., N. L. Poff, D. W. Baker, B. P. Bledsoe, D. M. Merritt, M. Lorie, G. T. Auble, et
 al. 2020. "Designing flows to enhance ecosystem functioning in heavily altered rivers."
 566 *Ecological Applications* 30: e02005.
- 567

570

- Bigelow, P. E. 2009. *Predicting areas of lake trout spawning habitat within Yellowstone Lake, Wyoming*. Doctoral dissertation, University of Wyoming, Laramie, Wyoming.
- 571 Bolker, B. 2008. *Ecological Models and Data in R*. Princeton University Press, Princeton.
- 572
 573 Bolker, B. 2022. "bbmle: Methods and Functions for Fitting Maximum Likelihood Models in
 574 R." R Package.
- 575
- 576 Brown, R. L., D. Charles, R. J. Horwitz, J. E. Pizzuto, K. Skalak, D. J. Velinsky, and D. D. Hart.
- 577 2024. "Size-Dependent Effects of Dams on River Ecosystems and Implications for Dam
- 578 Removal Outcomes." *Ecological Applications* 34: e3016.
- 579
- 580 Burnham, K. P., and D. R. Anderson. 1998. Model Selection and Inference: A Practical
- 581 *Information-Theoretic Approach.* Springer-Verlag, New York.
- 582

- 583 Chen, W., and J. D. Olden. 2017. "Designing Flows to Resolve Human and Environmental
- 584 Water Needs in a Dam-Regulated River." *Nature Communications* 8: 2158.
- 585
- 586 Cox, B. S. 2010. Assessment of an Invasive Lake Trout Population in Swan Lake, Montana.
- 587 Doctoral dissertation, Montana State University, Bozeman, Montana.
- 588
- 589 Crockett, H. J., B. M. Johnson, P. J. Martinez, and D. Brauch. 2006. "Modeling Target Strength
- 590 Distributions to Improve Hydroacoustic Estimation of Lake Trout Population Size."
- 591 *Transactions of the American Fisheries Society* 135: 1095–1108.
- 592

595

- 593 Crooks, J. A. 2005. "Lag Times and Exotic Species: The Ecology and Management of Biological
 594 Invasions in Slow-Motion." *Ecoscience* 12: 316–29.
- 596 Crooks, J. A., and M. E. Soule. 1999. "Lag Times in Population Explosions of Invasive Species:
- 597 Causes and Implications." In *Invasive Species and Biodiversity Management*, edited by O. T.
- Sandlund, P. J. Schei, and A. Viken, 103–125. Kluwer Academic Publishers, Boston,
 Massachusetts.
- 600
- Dai, A. 2013. "Increasing Drought under Global Warming in Observations and Models." *Nature Climate Change* 3: 52–58.
- 603
- Dettinger, M., B. Udall, and A. Georgakakos. 2015. "Western Water and Climate Change."
 Ecological Applications 25: 2069–2093.
- 606
 607 Dunham, J. B., C. Baxter, K. Fausch, W. Fredenberg, S. Kitano, I. Koizumi, K. Morita, et al.
 608 2008. "Evolution, Ecology, and Conservation of Dolly Varden, White-Spotted Char, and Bull
 609 Trout." *Fisheries* 33: 537–550.
- 610
- 611 Dux, A. M., C. S. Guy, and W. A. Fredenberg. 2011. "Spatiotemporal Distribution and
- 612 Population Characteristics of a Nonnative Lake Trout Population, with Implications for
- 613 Suppression." *North American Journal of Fisheries Management 31*: 187–196.
- 614
- 615 Ehsani, N., C. J. Vorosmarty, B. M. Fekete, and E. Z. Stakhiv. 2017. "Reservoir Operations
- under Climate Change: Storage Capacity Options to Mitigate Risk." *Journal of Hydrology* 555:
- **617 435–446**.
- 618
- Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D.
- 620 W. Chess, et al. 2011. "Long-Term Effects of a Trophic Cascade in a Large Lake Ecosystem."
- 621 *Proceedings of the National Academy of Sciences, United States* 108: 1070–1075.
- 622
- Eloranta, A. P., J. Sanchez-Hernandez, P.-A. Amundsen, S. Skoglund, J. M. Brush, E. H.
- Henriksen, and M. Power. 2016. "Water Level Regulation Affects Niche Use of a Lake Top
- 625 Predator, Arctic Charr (*Salvelinus alpinus*)." *Ecohydrology* 10: e1766.
- 626
- Essington, T. E. 2021. Introduction to Quantitative Ecology. Oxford University Press, New 627 York.
- 628
- 629
- 630 Evtimova, V. V., and I. Donohue. 2016. "Water-Level Fluctuations Regulate the Structure and Functioning of Natural Lakes." Freshwater Biology 61: 251-264. 631
- 632
- Felts, E. A., M. J. Fincel, and B. D. S. Graeb. 2020. "Effects of Reservoir Elevation and Spatial 633
- Synchrony on Walleye Recruitment in Lake Oahe, Missouri River." North American Journal of 634 Fisheries Management 40: 1133–1145. 635
- 636
- Fitzsimons, J., G. Fodor, B. Williston, H. Don, B. Gray, M. Benner, T. Breedon, et al. 2005. 637 "Deepwater Spawning by Lake Trout (Salvelinus namaycush) in Keuka Lake, New York." 638 Journal of Great Lakes Research 31: 1–10. 639
- 640
- Gaboury, M. N., and J. W. Patalas. 1984. "Influence of Water Level Drawdown on the Fish 641 Populations of Cross Lake, Manitoba." Canadian Journal of Fisheries and Aquatic Sciences 41: 642
- 118-125. 643
- 644
- Gunn, J. M. 1995. "Spawning Behavior of Lake Trout: Effects on Colonization Ability." Journal 645 646 of Great Lakes Research 21: 323–329.
- 647
- Hansen, A. G. 2018. Coldwater Lake and Reservoir Research Projects. Annual Report, Colorado 648 649 Parks and Wildlife, Fort Collins, Colorado.
- 650
- Hansen, A. G., J. R. Gardner, K. A. Connelly, M. Polacek, and D. A. Beauchamp. 2022. 651
- "Trophic Compression of Lake Food Webs under Hydrologic Disturbance." *Ecosphere* 9: 652 e02304. 653
- 654
- Hansen, A. G., J. R. Gardner, K. A. Connelly, M. Polacek, and D. A. Beauchamp. 2022. 655
- "Resource Use among Top-Level Piscivores in a Temperate Reservoir: Implications for a 656 Threatened Coldwater Specialist." Ecology of Freshwater Fish 31: 469-491. 657
- 658
- 659 Hansen, M. J., N. J. Horner, M. Liter, M. P. Peterson, and M. A. Maiolie. 2008. "Dynamics of an Increasing Lake Trout Population in Lake Pend Oreille, Idaho." North American Journal of 660
- Fisheries Management 28: 1160–1171. 661
- 662
- Hansen, A. G., J. M. Lepak, E. T. Cristan, W. M. Pate, and C. J. Farrell. 2021. Coldwater Lake 663 and Reservoir Research. Annual Report, Colorado Parks and Wildlife, Fort Collins, Colorado. 664
- 665
- Hansen, A. G., J. S. Thompson, L. N. Hargis, D. Brauch, and B. M. Johnson. 2019. "Predatory 666 Threat of Introduced Yellow Perch in a Salmonid Dominated Reservoir Food Web." North 667
- American Journal of Fisheries Management 39: 172–190. 668 669
- Horne, A. C., E. L. O'Donnell, M. Acreman, M. E. McClain, N. L. Poff, J. A. Webb, et al. 2017. 670
- 671 "Moving Forward-The Implementation Challenge for Environmental Water Management." In

- 672 *Water for the Environment: From Policy and Science to Implementation and Management,*
- edited by A. C. Horne, J. A. Webb, M. J. Stewardson, B. Richter, and M. Acreman, 649–673.
- 674 Elsevier Inc, Amsterdam.
- 675
- Janssen, J., J. E. Marsden, C. R. Bronte, D. J. Jude, S. P. Sitar, and F. W. Goetz. 2007.
- "Challenges to Deep-Water Reproduction by Lake Trout: Pertinence to Restoration in Lake
 Michigan." *Journal of Great Lakes Research* 33: 59–74.
- 679
- 580 Jeppesen, E., M. Meerhoff, K. Holmgren, I. Gonzalez-Bergonzoni, F. Teixeira-de Mello, S. A. J.
- 681 Declerck, L. De Meester, et al. 2010. "Impacts of Climate Warming on Lake Fish Community
- 682 Structure and Potential Effects on Ecosystem Function." *Hydrobiologia* 646: 73–90.
- 683
- 684 Jeppesen, E., T. Mehner, I. J. Winfield, K. Kangur, J. Sarvala, D. Gerdeaux, M. Rask, et al.
- 2012. "Impacts of Climate Warming on the Long-Term Dynamics of Key Fish Species in 24
 European Lakes." *Hydrobiologia* 694: 1–39.
- 687
- Johnson, B. M., L. Saito, M. A. Anderson, P. Weiss, M. Andre, and D. G. Fontane. 2004.
- "Effects of Climate and Dam Operations on Reservoir Thermal Structure." *Journal of Water Resources Planning and Management* 130: 112–122.
- 691
- Johnson, B. M., and J. M. Butteris. 2009. *Effects of an Anticipated Illegal Introduction of*
- 693 Walleye into Blue Mesa Reservoir, Colorado. Department of Fish, Wildlife and Conservation
- Biology, Colorado State University, Fort Collins, Colorado.
- 695
- Johnson, C. F., B. M. Johnson, T. E. Neebling, and J. C. Burckhardt. 2017a. "Walleye
- Introduction Eliminates Predation Refuge for Adfluvial Cutthroat Trout and Rainbow Trout."
 Transactions of the American Fisheries Society 146: 252–267.
- 699
- Johnson, B. M., and M. L. Koski. 2005. *Reservoir and Food Web Dynamics at Blue Mesa*
- 701 *Reservoir, Colorado, 1993-2002.* Department of Fishery and Wildlife Biology, Colorado State
 702 University, Fort Collins, Colorado.
- 703
- Johnson, B. M., and P. J. Martinez. 2000. "Trophic Economics of Lake Trout Management in
- Reservoirs of Differing Productivity." North American Journal of Fisheries Management 20:
 127–143.
- 707
- Johnson, B. M., W. M. Pate, and A. G. Hansen. 2017b. "Energy Density and Dry Matter Content in Fish: New Observations and an Evaluation of some Empirical Models." Transactions of the
- 710 American Fisheries Society 146: 1262–1278.
- 711
- Johnson, D. M., and R. G. Walsh. 1987. Economic Benefits and Costs of the Fish Stocking
- 713 *Program at Blue Mesa Reservoir, Colorado*. Technical Report No. 49. Colorado Water
- 714 Resources Research Institute, Colorado State University, Fort Collins, Colorado.
- 715

Kahl, U., S. Hulsmann, R. J. Radke, and J. Benndorf. 2008. "The Impact of Water Level 716 717 Fluctuations on the Year Class Strength of Roach: Implication for Fish Stock Management." *Limnologica* 38: 258–268. 718 719 Kovach, R. P., R. Al-Chokhachy, D. C. Whited, D. A. Schmetterling, A. M. Dux, and C. C. 720 721 Muhlfeld. 2017. "Climate, Invasive Species and Land Use Drive Population Dynamics of a 722 Coldwater Specialist." Journal of Applied Ecology 54: 638-647. 723 724 Lepak, J. M. 2013. Summer Profundal Index Netting (SPIN) for Lake Trout Population Estimates in Grand Lake and Taylor Park Reservoir. Colorado Parks and Wildlife, Fort Collins, Colorado. 725 726 Lindeløv, J. 2020. "mcp: An R Package for Regression with Multiple Change Points." R 727 728 Package. 729 Lynch, A. J., S. J. Cooke, A. M. Deines, S. D. Bower, D. B. Bunnell, I. G. Cowx, V. M. Nguyen, 730 et al. 2016. "The Social, Economic, and Environmental Importance of Inland Fish and 731 732 Fisheries." Environmental Reviews 24: 115-121. 733 Lynch, A. J., H. S. Embke, E. A. Nyboer, L. E. Wood, A. Thorpe, S. C. Phang, D. F. Viana, et al. 734 2024. "Inland Recreational Fisheries Contribute Nutritional Benefits and Economic Value but 735 are Vulnerable to Climate Change." *Nature Food* 5: 433–443. 736 737 Lytle, D. A., and N. L. Poff. 2004. "Adaptation to Natural Flow Regimes." *Trends in Ecology* 738 739 and Evolution 19: 94-100. 740 741 Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, et al. 2009. "Western Lake Trout Woes." Fisheries 34: 424-442. 742 743 McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. Lester, B. Shuter, et 744 al. 2016. "The Adaptive Capacity of Lake Food Webs: From Individuals to Ecosystems." 745 *Ecological Monographs* 86: 4–19. 746 747 748 Mims, M. C., and J. D. Olden. 2012. "Life History Theory Predicts Fish Assemblage Response to Hydrologic Regimes." Ecology 93: 35-45. 749 750 Miranda, L. E., G. Coppola, and J. Boxrucker. 2020. "Reservoir Fish Habitats: A Perspective on 751 Coping with Climate Change." Reviews in Fisheries Science and Aquaculture 28: 478–498. 752 753 754 Murphy, C. A., I. Arismendi, G. A. Taylor, and S. L. Johnson. 2019a. "Evidence for Lasting Alterations to Aquatic Food Webs with Short-Duration Draining." PLoS One 14: e0211870. 755 756 757 Murphy, C. A., G. Taylor, T. Pierce, I. Arismendi, and S. L. Johnson. 2019b. "Short-Term Reservoir Draining to Streambed for Juvenile Salmon Passage and Non-Native Fish Removal." 758 Ecohydrology 12: e2096. 759 760

761	Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. "Decline of the Migratory form in Bull
762	Charr, Salvelinus confluentus, and Implications for Conservation. Environmental Biology of
763	<i>Fishes</i> 64: 321–332.
764	
765	Nilsson, C., C. A. Reidy, M. Dynesius, and C. Ravenga. 2005. "Fragmentation and Flow
766	Regulation of the World's Large River Systems." <i>Science</i> 308: 405–408.
767	
768	Nuhold, J. M. and K. H. Lu. 1957. Creel Census Methods. Utah State Department of Fish and
769	Game. Publication No. 8. 36 pp.
770	
771	O'Connor, J. E., J. J. Duda, and G. E. Grant. 2015. "1000 Dams Down and Counting." Science
772	348: 496–97.
773	
774	Olden, J. D., C. P. Konrad, T. S. Melis, M. J. Kennard, M. C. Freeman, M. C. Mims, E. N. Bray,
775	et al. 2014. "Are Large-Scale Flow Experiments Informing the Science and Management of
776	Freshwater Ecosystems?" Frontiers in Ecology and the Environment 24: 176–185.
777	
778	Opperman, J. J., E. Kendy, and E. Barrios. 2019. "Securing Environmental Flows through
779	System Reoperation and Management: Lessons from Case Studies of Implementation." Frontiers
780	in Environmental Science 7: 104.
781	
782	Parisek, C. A., F. A. De Castro, J. D. Colby, G. R. Leidy, S. Sadro, and A. L. Rypel. 2024.
783	"Reservoir Ecosystems Support Large Pools of Fish Biomass." Scientific Reports 14: 9428.
784	
785	Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. "Managing for Coexistence of
786	Kokanee and Trophy Lake Trout in a Montane Reservoir." North American Journal of Fisheries
787	Management 34: 908–922.
788	
789	Piccolo, J. J., and W. A. Hubert, 1993, "Standard Weight Equation for Lake Trout," North
790	American Journal of Fisheries Management 13: 401–404.
791	
792	Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. "Homogenization of Regional
793	River Dynamics by Dams and Global Biodiversity Implications." Proceedings of the National
794	Academy of Sciences 104: 5732–5737.
795	
796	Powell, T. 1980. Fisherman Survey and Harvest Analysis. Job Segment Report, Colorado
797	Division of Wildlife, Denver, Colorado.
798	
799	R Core Team. 2023. "R: A Language and Environment for Statistical Computing." Vienna.
800	Austria: R Foundation for Statistical Computing. Available from: http://www.Rproject.org
801	[Accessed 16th August 2022].
802	L
803	Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd. et
804	al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater

805 Biodiversity." *Biological Reviews* 94: 849–873.

806

- Richter, B. D., and G. A. Thomas. 2007. "Restoring Environmental Flows by Modifying Dam
 Operations." Ecology and Society 12: 12.
- Rolls, R. J., B. Hayden, and K. K. Kahilainen. 2017. "Conceptualising the Interactive Effects of
- Climate Change and Biological Invasions on Subarctic Freshwater Fish." *Ecology and Evolution* 7: 4109–4128.
- 813
- 814 Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. "Effects of Introduced Lake Trout on
- 815 Native Cutthroat Trout in Yellowstone Lake." *Ecological Applications* 13: 23–37.
- 816
- Saito, L., B. M. Johnson, J. Bartholow, and R. B. Hanna. 2001. "Assessing Ecosystem Effects of
 Reservoir Operations using Food Web-Energy Transfer and Water Quality Models." *Ecosystems*4: 105–125.
- 820
- Sandstrom, S. J., and N. Lester. 2009. *Summer Profundal Index Netting Protocol: A Lake Trout Assessment Tool*. Ontario Ministry of Natural Resources, Peterborough.
- 823
- Schiermeier, Q. 2018. "Dam Removal Restores Rivers." *Science* 557: 290–291.
- 826 Schindler, D. E. 2012. "The Dilemma of Controlling Cultural Eutrophication of Lakes."
- 827 Proceedings of the Royal Society B: Biological Sciences 279: 4322–4333.
- 828
- Schisler, G. J., and D. Bowden. 2012. *Creel Survey Design and Analysis Manual*. Colorado
 Parks and Wildlife, Aquatic Research Section, Fort Collins, Colorado.
- 831
- 832 Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. "Quantifying Latent Impacts of an
- 833 Introduced Piscivore: Pulsed Predatory Inertia of Lake Trout and Decline of Kokanee."
- 834 *Transactions of the American Fisheries Society* 141: 1191–1206.
- 835
- Scott, W. B., and E. J. Crossman. 1973. "Freshwater Fishes of Canada." *Fisheries Research Board of Canada*, Bulletin No. 184.
- 838
- Tickner, D., J. J. Opperman, R. Abell, M. Acreman, A. H. Arthington, S. E. Bunn, S. J. Cooke, et
 al. 2020. "Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery
 Plan." *BioScience* 70: 330–342.
- 842
- Tunney, T. D., K. S. McCann, N. P. Lester, and B. J. Shuter. 2014. "Effects of Differential
- Habitat Warming on Complex Communities." *Proceedings of the National Academy of Sciences of the* USA 111: 8077–8082.
- 846
- 847 Turley, L., C. Brethaut, and G. Pflieger. 2022. "Institutions for Reoperating Reservoirs in Semi-
- 848 Arid Regions Facing Climate Change and Competing Societal Water Demands: Insights from
- 849 Colorado." *Water International* 47: 30–54.
- 850

- Tyus, H. M. 1992. "An Instream Flow Philosophy for Recovering Endangered Colorado River Fishes." *Rivers* 3: 27–36.
- 853
- Van Buren, R. S., and W. T. Burkhard. 1981. *Final Report for Kokanee Salmon Study of the Blue Mesa Peaking Power Modification Project*. Colorado Division of Wildlife, Grand Junction,
- 856 Colorado.857
- 858 Van Steeter, M. M., and J. Pitlick. 1998. "Geomorphology and Endangered Fish Habitats of the
- 859 Upper Colorado River 1. Historic Changes in Streamflow, Sediment Load, and Channel
- 860 Morphology." *Water Resources Research* 34: 287–302.
- 861
- Vorosmarty, C. J., P. Green, J. Salisbury, and R. B. Lammers. 2000. "Global Water Resources:
 Vulnerability from Climate Change and Population Growth." *Science* 289: 284–288.
- 864865 Warnock, W. G., J. L. Thorley, S. K. Arndt, T. J. Weir, M. D. Neufeld, J. A. Burrows, and G. F.
- 866 Andrusak. 2022. "Kootenay Lake Kokanee (*Oncorhynchus nerka*) Collapse into a Predator Pit."
- 867 *Canadian Journal of Fisheries and Aquatic Sciences* 79: 234–238.
- 868
- Watts, R. J., B. D. Richter, J. J. Opperman, and K. H. Bowmer. 2011. "Dam Reoperation in an
 Era of Climate Change." *Marine and Freshwater Research* 62: 321–327.
- 871
- 872 Wiltzius, W. J. 1974. Post-Impoundment Fishery Investigations, Curecanti Unit, Upper
- 873 *Colorado Storage Project*. Final Report, Colorado Division of Wildlife, Fort Collins, Colorado.
- 874
- 875 Wiltzius, W. J. 1978. Some Factors Historically Affecting the Distribution and Abundance of
- 876 Fishes in the Gunnison River. Fishery Investigations of the Lower Gunnison River Drainage,
- 877 Final Report. Colorado Division of Wildlife, Fort Collins, Colorado.
- 878
- Yarnell, S. M., G. E. Petts, J. C. Schmidt, A. A. Whipple, E. E. Beller, C. N. Dahm, P. Goodwin,
 and J. H. Viers. 2015. "Functional Flows in Modified Riverscapes: Hydrographs, Habitats and
- 880 881
- Zohary, T., and I. Ostrovsky. 2011. "Ecological Impacts of Excessive Water Level Fluctuations
- in Stratified Freshwater Lakes." *Inland Waters* 1: 47–59.

Opportunities." BioScience 65: 963-972.

TABLES

TABLE 1. Parameter estimates (95% CIs in parentheses) for the one- and two-stage models. E flows = environmental flows. The winter creel survey period was January—April. The standard
 creel survey period was May—October.

Parameter	Description	One-stage model	Two-stage model
S ₀₋₃	Mean stocking survival from age-0 to age-3 for all cohorts	0.027 (0.020-0.035)	0.108 (0.070-0.157)
r or r_{trad}	Intrinsic productivity for one-stage model (<i>r</i>) or under traditional operations for two-stage model (<i>r</i> _{trad})	0.455 (0.425-0.576)	0.032 (-0.036-0.127)
<i>r</i> _{ef}	Intrinsic productivity for two-stage model under operations for e-flows	Not estimated	0.375 (0.309-0.481)
μ_{w-trad}	Winter exploitation rate under traditional operations	0.059 (0.028-0.135)	0.036 (0.018-0.069)
$\mu_{w\text{-}ef}$	Winter exploitation rate under operations for e-flows	0.104 (0.077-0.135)	0.090 (0.063-0.117)
$\mu_{STND-trad}$	Standard exploitation rate under traditional operations	0.438 (0.352-0.527)	0.127 (0.083-0.164)
$\mu_{STND-ef}$	Standard exploitation rate under operations for e-flows	0.277 (0.230-0.343)	0.222 (0.175-0.285)
q_{w-trad}	Winter catchability coefficient under traditional operations	0.00221 (0.00104-0.00439)	0.00185 (0.00090-0.00389)
q_{w-ef}	Winter catchability coefficient under operations for e-flows	0.00528 (0.00321-0.00839)	0.00437 (0.00282-0.00672)
$q_{\it STND-trad}$	Standard catchability coefficient under traditional operations	0.00289 (0.00202-0.00396)	0.00098 (0.00070-0.00141)
$q_{\mathit{STND-ef}}$	Standard catchability coefficient under operations for e-flows	0.00224 (0.00159-0.00299)	0.00175 (0.00145-0.00229)

890 FIGURE CAPTIONS

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; panel B). Releases were scaled by dividing each monthly
 mean by the corresponding reservoir inflow (CMS). (C) Time series of reservoir surface

- mean by the corresponding reservoir inflow (CMS). (C) 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. (D) Time series for the magnitude of fall-to-spring flux
- for each operational regime (points) and the fitted change-point regression model identifying
- 899 distinct regimes (gray line). Photo credit: Adam Hansen.
- 900

FIGURE 2. History of the Blue Mesa Reservoir fishery. (A) Times series of angler catch rates
 (CPAH) for lake trout based on total fishing efforts (boat & bank) estimated during the standard

903 open-water May-October creel survey period. Blue asterisks indicate years when lake trout

- fingerlings were stocked. (B) Corresponding catches and harvests of lake trout and fall removals.
- The inset panel shows the length structure of lake trout observed in the standard creel from 1993-
- 2012. (C) Angler catch rates of kokanee and boat fishing efforts during the standard creel periodand pelagic prey abundances (primarily reflective of kokanee) derived from standard
- 908 hydroacoustics surveys. (D) Corresponding creel catches and harvests of kokanee and total
- numbers of fingerlings stocked annually. (E) Length-dependent body condition of lake trout
- based on the relative weight index (Piccolo & Hubert, 1993) observed in the year 2000, when
- kokanee abundance was near its peak, and in 2009 when kokanee collapsed. Lines are fitted
- 912 linear regression models. (F) Total number of kokanee eggs collected from the fall spawning run
- at Roaring Judy Hatchery upstream of the reservoir. Photo credit: (A) Bill Pate, Colorado State
- 914 University (CSU). (C) Lisa Lynch, National Park Service. (D & E) Brett Johnson, CSU. (F)
- 915 Kevin Rogers, Colorado Parks and Wildlife. Data are provided in Tables S1 through S5 of
- 916 Supporting Information.
- 917

FIGURE 3. Fits of the one- and two-stage models to the time series of fisheries-independent

- 919 (abundance from mark-recapture and SPIN) and dependent (angler creel) survey data from Blue
- 920 Mesa Reservoir. (A) Catchable lake trout abundance. (B) Catch-per-angler hour (CPAH) during
- 921 the winter ice and ice-off creel period (January–April). (C) Winter harvest. (D) CPAH during
- 922 the standard creel period (May–October). (E) Standard harvest. The vertical line on each panel
- marks 1988 when change point regression identified a regime shift in the magnitude of fall-to-
- 924 spring flux.

925 FIGURES





929 FIGURE 2.



SUPPLEMENTAL INFORMATION 932

933

Table S1. 934

Table S1. Time series of fisheries survey data for lake trout in Blue Mesa Reservoir, Colorado, USA. The standard creel period was from May–October. Winter creel period was from January–April.

		Total standard		CPAH													
		effort (1,000		(fish/1,000													
	e. 1.	angler hours	C 1 1	angler hours	CV for		CV for	Winter effort		Winter CPAH	CV for		CV for		CV for		
	Fingerlings	of boat and	Standard	of boat and	standard	Standard	standard	(1,000 angler	winter	(fish/1,000	winter	winter	winter	Catchable	catchable	Fall	
1069	28,000	Dank fishing)	catch	Dank fishing)	СРАН	narvest	narvest	nours)	catch	angier nours)	CPAH	narvest	narvest	abundance	abundance	removais	-
1900	28,000															0	
1909	0															0	
1970	0	379 30	3 1 3 7	8 27	0 30*	808	0.32									0	
1072	35 300	373.30	3,137	0.04	0.35	775	0.32									0	
1972	33,200	333.46	5,514	9.94	0.59	775	0.52									0	
1973	24,960	290.55	1,694	5.83	0.39*	502	0.32									0	
1974	18,060	250.33	1,464	5.85	0.39*	523	0.32									0	
1975	0	232.42	1,090	4.69	0.39*	366	0.32									0	
1976	0	256.90	971	3.78	0.39*	355	0.32									0	
1977	0	221.75	1,002	4.52	0.39*	381	0.32									0	
1978	0															0	
1979	0															0	
1980	0	331.50	540	1.63	0.26	540	0.19									0	
1981	0															0	
1982	0	432.07	1,864	4.31	0.53	1,767	0.52									0	
1983	0															0	
1984	0							37.54	52	1.38	0.51	52	0.43			0	
1985	0															0	
1986	0							39.29	592	15.06	0.45	331	0.52			0	
1987	0															0	
1988	10,000															0	
1989	0	431.96	19	0.04	1.03	19	1.00									0	
1990	0															0	
1991	0															0	
1992	24,709															0	
1993	0	352.62	5,187	14.71	0.31	3,873	0.25									0	
1994	0	336.33	269	0.80	0.69	252	0.65									0	
1995	0	278.95	2,901	10.40	0.53	2,242	0.26									0	
1996	0	235.42	695	2.95	0.50	675	0.47									0	
1997	0	233.25	1,033	4.43	0.45	754	0.33									0	
1998	0	245.57	1,365	5.56	0.31	1,001	0.29									0	
1999	0	260.91	3,470	13.30	0.31	2,331	0.22									0	
2000	0	312.57	2,019	6.46	0.31	1,186	0.24									0	
2001	0	194.18	2,687	13.84	0.52	5//	0.34							40 746	0.17	0	
2002	0	232.91	5,173	22.21	0.36	3,590	0.41							10,716	0.47	0	
2003	0	206.54	4,639	22.46	0.45	2,560	0.23	22.02	~		0.04	4 220				0	
2004	0	209.82	4,799	22.87	0.43	3,130	0.32	23.03	2,144	93.11	0.81	1,229	0.24			0	
2005	0	246.35	3,249	13.19	0.32	1,986	0.33	20.51	2 0 2 0	05.00	0.22	1 470	0.10			0	
2006	0	105.71	4,078	28.23	0.22	2,502	0.13	30.51	2,928	95.98	0.32	1,479	0.18			0	
2007	0	191.92	0,700	55.22	0.22	4,009	0.10									0	
2006	0	147.10	0,050	21 54	0.20	4,415	0.17									014	
2009	0	172.90	5,455	42.24	0.20	4,232	0.25									914	
2010	0	155.10	3,723	42.54	0.22	5,670	0.14							24.074	o ac‡	1,519	
2011	U	166.87	7,182	43.04	0.23	5,670	0.15	20.41	1.005	67.54	0.21	1.057	0.21	34,071	0.36	1,170	
2012	U	161.77	4,096	25.32	0.27	2,188	0.24	29.41	1,985	67.51	0.31	1,857	0.21			/3/	
2013	U														[‡]	1,278	
2014	U													26,753	0.36	1,632	
2015	U															1,400	
2016	0													24,368	0.36*	911	
2017	0															429	
2018	0													24,455	0.36*	0	_
*Average	CV from star	ndard creel CPA	H estimates	1980 and later.													

*Average CV from strandard creel harvest estimates 1980 and later.

*The recommended approach for characterizing uncertainty in density/abundance estimates from Summer Profundal Index Netting (SPIN) underestimates error (Sandstrom & Lester, 2009). There -

References:

Bonar, S. A., Hubert, W. A., and D. W. Willis. 2009. Standard Methods for Sampling North American Freshwater Fishes . American Fisheries Society, Bethesda, Maryland.

Giacomini, H. C., N. Lester, P. Addison, S. Sandstrom, D. Nadeau, C. Chu, and D. de Kerckhove. 2020. "Gillnet Catchability of Walleye (Sander vitreus): Comparison of North American and Provincial Standards." Fisheries Research 224: 105433.

Hansen, A. G., M. M. Miller, E. T. Cristan, C. J. Farrell, P. Winkle, M. M. Brandt, K. D. Battige, K.D., et al. 2023. "Gill Net Catchability of Walleye (Sander vitreus): Are Provincial Standards Suitable for Estimating Adult Density Outside the Region?" Fisheries Research 266: 106800.

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Sandstrom, S. J., and N. Lester. 2009. Summer Profundal Index Netting Protocol: A Lake Trout Assessment Tool (version 2009.1). Ontario Ministry of Natural Resources, Peterborough.

Total hender Loo 110 120 130 140 150 <t< th=""><th>Table S2. Length-freque</th><th>ncy dist</th><th>tributi</th><th>ons of</th><th>lake tr</th><th>out sar</th><th>npled</th><th>from th</th><th>ne angl</th><th>er cree</th><th>l annu</th><th>ally fro</th><th>m 199</th><th>3-2012</th><th>in Blu</th><th>e Mesa</th><th>Reser</th><th>voir, C</th><th>olorad</th><th>o, USA.</th><th></th></t<>	Table S2. Length-freque	ncy dist	tributi	ons of	lake tr	out sar	npled	from th	ne angl	er cree	l annu	ally fro	m 199	3-2012	in Blu	e Mesa	Reser	voir, C	olorad	o, USA.	
cond cond <th< th=""><th></th><th>Count</th><th>L ITEQU</th><th>encies</th><th>420</th><th>4.40</th><th>450</th><th>4.00</th><th>470</th><th>100</th><th>100</th><th>200</th><th>24.0</th><th>220</th><th>220</th><th>240</th><th>250</th><th>260</th><th>270</th><th>200</th><th>200</th></th<>		Count	L ITEQU	encies	420	4.40	450	4.00	470	100	100	200	24.0	220	220	240	250	260	270	200	200
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2010 2 22 3 7 7 1 9 3 5 3 5 6 1 2 0 2 0 2 1 1 2011 11 7 2 1 1 12 0 5 2 1 3 1 1 1 1 1 2012 11 4 9 5 5 10 4 4 2 4 1 1 7 2 1 1	2009	3	5	5	2	1	1	1	1		1		1			1			1		1
2011 11 7 2 1 1 1 1 1 1 2012 11 4 9 5 5 10 4 4 2 4 1 1 7 2 1	2010	2	22	3	7	7	1	9	3	5	3		5	6	1	2	0	2	0	2	1
2012 11 4 9 5 5 10 4 4 2 4 1 1 1 7 2 1 1	2011	11	7	2	1	1	12	0		5	2	1	3	1	1		1			1	
	2012	11	4	9	5	5	10	4	4	2	4	1	1	1	7	2	1	1			

938 Table S2 continued.

Table S2. Length-freque	ncy dist	ributio	ons of I	ake tro	out san	npled f	rom th	e angl	er cree	l annu	ally fro	m 1993	3-2012	in Blue	e Mesa	Reserv	/oir, Co	olorado	o, USA.	
	Count	freque	encies																	
Total length bin (mm):	700	710	720	730	740	750	760	770	780	790	800	810	820	830	840	850	860	870	880	890
Year:																				
1993																				
1994																				
1995																				
1996																				
1997																				
1998				1			1			1			1				0			
1999	1	2			3		6			2	0	3		0	0		2		0	0
2000	2		1														1			
2001	0				0	1		0		1		0	1							
2002						2						1								
2003	3					2	1	1	2					1			1			
2004	1	1		1		1	3				0	2	1						3	
2005		2			0			0		1		0								1
2006		1			1			0				1	1					1		
2007	2		1																	
2008			1		1												1			
2009			2			2									1					
2010	2	0	1	1	0	0	2	1		1	1	1	1	0	0		1	0	1	
2011								0	1						1					
2012	0	1	0			0		1	2	0			1		3		0		1	0
Total length bin (mm):	900	910	920	930	940	950	960	970	980	990	1000	1010	1020	1030	1040	1050				
Year:																				
1993																				
1994																				
1995																				
1996																				
1997																				
1998				1			0													
1999	1	0			0															
2000		1					1													
2001		0	1										0							
2002																				
2003		1						1					1							
2004			1								1	1	0		1					
2005			1										1							
2006																				
2007																				
2008											0									
2009		1				1		1												
2010		1	1				1				2					1				
2011											0									
2012	0		0	2			1	1						1						

Table S3.

Table S3. Spring body condition of lake trout in Blue Mesa Reservoir, Colorado, USA, whenkokanee were near peak abundance (2000), and in the year kokanee collapsed (2009).YearTotal length (mm) ± SDRelative weight ± SDN

	Year	Total length (mm) ± SD	Relative weight ± SD	N	
_	2000	634.8 ± 139.4	109.0 ± 23.1	339	
942 _	2009	550.2 ± 141.9	84.5 ± 12.8	1265	
-					

943 **Table S4.**

Table S4. Fisheries survey data for kokanee observed during the lake trout expansion period (1990 and later) in Blue Mesa Reservoir, Colorado, USA. The standard creel period was from May—October.

	Hydropcoustics based	Total standard effort	Standard catch	Standard CPAH	CV for	Standard baruost	CV for standard
Vear	abundance (1 000s)	(1,000 boat lisining	(1 000s)	(IISH) 1,000 DOAL	standard CPAH	(1 000s)	harvest
1990	abunuance (1,0003)	nours	(1,0003)	1100137	Standard CLAI	(1,0003)	narvest
1991							
1992							
1993		285.71	171.91	601.71	0.10	149.22	0.10
1994	941.23	277.51	153.81	554.24	0.11	148.12	0.11
1995	354.91	235.63	105.64	448.32	0.28	99.62	0.30
1996	417.42	206.29	70.88	343.61	0.05	69.54	0.05
1997	281.40	204.75	70.39	343.79	0.12	65.68	0.11
1998	307.45	198.70	60.24	303.19	0.17	56.21	0.18
1999	530.29	202.44	55.57	274.49	0.13	50.01	0.14
2000	842.01	257.65	128.12	497.26	0.09	113.77	0.08
2001	1026.40	165.77	84.63	510.56	0.08	73.63	0.09
2002	509.42	206.79	129.86	628.01	0.11	122.07	0.12
2003	412.01	188.49	85.20	452.03	0.09	80.09	0.09
2004	550.37	191.70	62.70	327.09	0.16	58.31	0.16
2005	468.62	215.93	85.92	397.91	0.10	73.89	0.09
2006	503.16	146.66	53.07	361.87	0.18	47.76	0.12
2007	299.88	170.28	59.17	347.49	0.13	53.85	0.07
2008	159.18	127.62	32.95	258.17	0.16	30.31	0.09
2009	109.53	149.30	30.54	204.55	0.13	29.62	0.07
2010	273.95	111.98	22.93	204.79	0.16	20.64	0.11
2011	288.46	138.77	44.49	320.64	0.17	39.60	0.10
2012	284.48	136.13	68.87	505.88	0.11	59.23	0.06
2013	162.66						
2014							
2015	412.72						
2016	376.53						
2017							
2018	442.77						
2019	426.07						
2020							

Table S5.

 Table S5. Times series of kokanee fingerling stockings and eggs collected at the hatchery upstream

 of Blue Mesa Reservoir, Colorado, USA.

Year	Kokanee fingerlings stocked (millions)	Kokanee eggs collected at hatchery (millions)
1965	0.050	
1966	0.533	
1967	1.360	
1968	0.645	
1969	0.638	0.088
1905	0.000	2.040
1970	1 010	0.624
1971	1.019	0.034
1972	0.915	2.037
1973	1.000	0.106
1974	2.172	0.602
1975	1.079	0.982
1976	1.039	1.385
1977	0.891	1.600
1978	0.951	0.350
1979	0.698	1.966
1980	1.385	0.300
1981	1.426	1.500
1982	2.128	1.281
1983	1.570	3.312
1984	2.217	0.887
1985	2.556	2.719
1986	2.000	2.605
1987	1.896	2.676
1988	1.530	3.128
1989	1.453	5.128
1990	1 450	5 178
1991	1 350	A 231
1992	1.550	4.231
1003	1 370	9.225
1993	1.09	7,400
1994	1.408	9.250
1995	1.700	a.550 7.840
1990	2.100	7.840
1997	1.976	5.590
1998	2.249	5.405
1999	3.000	4.418
2000	3.054	7.614
2001	3.182	4.408
2002	2.781	7.263
2003	3.023	5.987
2004	2.890	2.721
2005	2.710	7.233
2006	2.826	7.435
2007	2.942	8.270
2008	2.852	5.846
2009	3.307	2.438
2010	3.416	5.351
2011	3.541	11.035
2012	3.582	13.122
2013	3.483	7.511
2014	3,439	2.851
2015	3 597	2 1/3
2015	3.557	17 225
2010	3.347	16 704
2017	2.043	10.704
2018	3.531	9.205
2019	3.490	6.456
2020	3.4/6	1.930

Table S6.

°p _{i,j} = 1.0%											
Parameter	Estimate	Lower 95% Cl	Upper 95% Cl								
S ₀₋₃	0.108	0.070	0.157								
r _{trad}	0.032	-0.036	0.127								
r _{ef}	0.375	0.309	0.481								
$\mu_{\textit{w-trad}}$	0.036	0.018	0.069								
μ_{w-ef}	0.090	0.063	0.117								
$\mu_{\textit{STND}-trad}$	0.127	0.083	0.164								
$\mu_{\textit{STND}-ef}$	0.222	0.175	0.285								
q _{w-trad}	0.00185	0.00090	0.00389								
q _{w-ef}	0.00437	0.00282	0.00672								
q _{STND} -trad	0.00098	0.00070	0.00141								
q _{STND} -ef	0.00175	0.00145	0.00229								

986 Table S6. Parameter estimates for the two-stage model under varying degrees of creel survey bias toward nearshore fishes.

ĵp _{i,j} = 0.5%										
Parameter	Estimate	Lower 95% Cl	Upper 95% Cl							
S ₀₋₃	0.088	0.062	0.131							
r _{trad}	0.046	-0.020	0.148							
r _{ef}	0.379	0.327	0.454							
$\mu_{\textit{w-trad}}$	0.034	0.017	0.066							
μ_{w-ef}	0.090	0.072	0.123							
$\mu_{\textit{STND}-trad}$	0.118	0.087	0.150							
$\mu_{_{STND}-ef}$	0.224	0.177	0.283							
q_{w-trad}	0.00174	0.00085	0.00362							
q _{w-ef}	0.00441	0.00283	0.00678							
q _{STND} -trad	0.00091	0.00067	0.00144							
q _{STND} -ef	0.00177	0.00135	0.00211							

ĵp _{i,j} = 1.5%										
Parameter	Estimate	Lower 95% Cl	Upper 95% Cl							
S ₀₋₃	0.146	0.098	0.204							
r _{trad}	0.010	-0.062	0.118							
r _{ef}	0.366	0.304	0.447							
$\mu_{\textit{w-trad}}$	0.045	0.021	0.114							
μ_{w-ef}	0.088	0.064	0.125							
$\mu_{\textit{STND-trad}}$	0.144	0.108	0.211							
$\mu_{\textit{STND}-ef}$	0.217	0.176	0.294							
q _{w-trad}	0.00236	0.00107	0.00626							
q _{w-ef}	0.00428	0.00267	0.00671							
q _{STND} -trad	0.00113	0.00083	0.00167							
q _{STND} -ef	0.00172	0.00134	0.00201							

<u>RESEARCH PRIORITY</u>:

Understanding Gizzard Shad (*Dorosoma cepadianum*) in Colorado. Report: Gizzard Shad (*Dorosoma cepedianum*) 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.

INTRODUCTION

Gizzard Shad *Dorosoma cepedianum* 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.

PROJECT PROGRESS

A report entitled "Gizzard Shad (*Dorosoma cepedianum*) in Colorado lakes, reservoirs and ponds: background, generalizations, system-specific examples, control, and alternatives", is being drafted. The draft report currently contains 10 sections that include: 1) Gizzard Shad background, 2) Gizzard Shad in Colorado, 3) Data limitations, 4) Generalizations: Gizzard Shad

success/persistence, 5) System-specific Gizzard Shad catch rates, 6) System-specific Gizzard Shad catch rate inference, 7) Disadvantaging/controlling Gizzard Shad, 8) Alternative species, and 10) Conclusions. The report will also include an appendix describing data limitations and recommendations for data entry moving into the future. These sections are being refined, and two more sections dealing with Gizzard Shad transplants and Gizzard Shad hatching in Chatfield and Cherry Creek reservoirs are being developed. The report is projected for completion in the 2024-2025 fiscal year.

REFERENCES

Fetzer, W. W., T. E. Brooking, J. R. Jackson, and L. G. Rudstam. 2011. Overwinter mortality of Gizzard Shad: evaluation of starvation and cold temperature stress. Transactions of the American Fisheries Society 140(6):1460-1471.

Miller, R. R. 1960. Systematics and biology of the Gizzard Shad (*Dorosoma cepedianum*) and related fishes. Fishery Bulletin 173. Fishery Bulletin of the Fish and Wildlife Service Volume 60.

Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52(11):2518-2526.

<u>RESEARCH PRIORITY</u>:

Informing angler harvest incentive programs: Using models to examine the biological efficacy of incentivized angling/harvest for controlling invasive, nuisance or managed nonnative sport fishes.

OBJECTIVES

To prepare and submit a manuscript that uses simulation models to explore the potential biological efficacy of incentivized harvest for controlling nuisance Smallmouth Bass *Micropterus salmoides* in Elkhead and Ridgway reservoirs. Use the models to identify potential avenues for increasing program efficacy.

MANUSCRIPT

Hansen, A. G., J. M. Lepak, E. I. Gardunio, and T. Eyre. Evaluating harvest incentives for suppressing a socially-valued, but ecologically-detrimental, invasive fish predator. Fisheries Management and Ecology. 31(4):e12699.

BACKGROUND

There are no documented attempts to control invasive Smallmouth Bass using cost-effective harvest incentive programs alone. Yet, this approach integrates anglers into the control process directly, and can facilitate outreach and education. This approach could be effective under conditions that facilitate success, such as in small systems combined with adequate resources/funding and motivated natural resource managers. The primary objective of this study was to evaluate the potential biological efficacy of incentivized harvest for controlling introduced Smallmouth Bass in two small reservoirs (<400 ha) within the Colorado River basin. To address this objective, we quantified the harvest dynamics of anglers during a series of incentive-based fishing tournaments on each reservoir.

MANUSCRIPT ABSTRACT

The legacy of intentional freshwater fish introductions across the western United States has fostered social tensions over the control of nonnative species in some contexts. Overcoming tensions and implementing effective control programs is important for mitigating impacts to native species. We modeled the efficacy of incentivized harvest for controlling nuisance Smallmouth Bass (*Micropterus dolomieu*) using empirical responses measured during fishing tournaments on two reservoirs that are sources of nonnative predators to critical habitat of native species. Simulations demonstrated that anglers could suppress adult Smallmouth Bass by 90%–99% in under 30 years, but were contingent on program participation and density dependence in harvest efficiency (i.e., catchability) and population demographics. Catchability differed between systems and varied temporally within the same system, thereby suggesting tournament structure could be adapted to increase harvest rates. Incentivized harvest should not be dismissed as a viable control strategy alone or in tandem with other methods in small lentic systems.

<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, 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.

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) 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, 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

- Over 15,000 tiger muskellunge have been stocked in Shadow Mountain Reservoir (2023 and 2024) and several have been recovered (those stocked in 2023) indicating that some individuals are surviving and growing. At stocking in 2023, mean lengths and weights of tiger muskellunge stocked were 203 mm and 44 grams.
- On 3 and 4 June 2024 a routine gillnetting survey (n = 20 nets set for 6 hours each) was conducted in Shadow Mountain Reservoir and catch rates of White Suckers remained elevated as observed in the past (no notable effect from stocked tiger muskellunge). Samples for stable isotope baselines were also collected (Brown Trout, Fathead Minnow, Iowa Darter, and White Sucker). Two tiger muskellunge were captured that were stocked in 2023 measuring 244 and 275 mm and weighing 93 and 119 grams that originated from Pennsylvania and Nebraska, respectively. Brook Trout, Brown Trout, and Rainbow Trout captured appeared to be in better condition than previous years (J. Ewert pers. comm.).
- On 5 June 2024 an opportunistic boat electrofishing survey was conducted to collect tiger muskellunge for future analyses. Five tiger muskellunge were captured that were stocked in 2023. Two individuals were from Pennsylvania (250 and 280 mm weighing 97 and 132 grams), one individual was from Nebraska (280 mm and 126 grams), and two individuals were untagged (stocked in 2023) and smaller (~200 mm and 65 grams).

- The mean lengths and weights for all Pennsylvania and Nebraska tiger muskellunge caught in Shadow Mountain Reservoir in 2024 were 258 mm and 107 grams, and 278 mm and 123 grams respectively.
- All 3,700 tiger muskellunge from Nebraska intended for stocking in Shadow Mountain Reservoir were tagged in August with PIT tags at the CPW hatchery in Wray. Tagging was successful with low mortality (11 mortalities of 3,700), similar to what was observed for tiger muskellunge originating from Pennsylvania (~0.3% mortality) in 2023.
- On 28 August 2024, 3,700 tiger muskellunge were stocked into Shadow Mountain Reservoir. The fish were stocked by boat and distributed in protected areas with structure around the islands of Shadow Mountain Reservoir on the southern end.
- In October and November 2024 three tiger muskellunge (stocked in 2023) were found dead against a kokanee salmon trap during the egg-take operation. Individuals were 464, 470, and 506 mm. One tagged individual was from Pennsylvania and was stocked in a batch with a mean length of 205 mm. The individual (pictured below, image credit: J. Ewert) was 470 mm. Catches of similar and larger-sized tiger muskellunge have been reported to Biologist J. Ewert, indicating relatively rapid growth.



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) crayfish and White Crappie were collected in a range of sizes to establish stable isotope baselines.

- Boat electrofishing was conducted in Elkhead Reservoir in Mid-June to mark Smallmouth Bass for the annual angler incentivized tournament. Individuals were fin clipped and released to gain information about the Smallmouth Bass population and the efficacy of control measures.
- During boat electrofishing in Elkhead Reservoir (described above), two tiger muskellunge were captured measuring 376 and 382 mm. These fish were stocked earlier in the year in mid-April as holdovers (held in the hatchery over winter and raised to a larger size for spring stocking) with approximately the same mean length as these two tiger muskellunge.
- Holdover (~500 mm) tiger muskellunge (n = 200) were tagged with PIT tags in April at the Wray Hatchery and stocked in Elkhead Reservoir on 22 April 2024. Tagging was successful with no short-term mortality observed, similar to what was observed during tagging in 2023.
- Small (~200 mm) tiger muskellunge (n = 1,826) were tagged with Floy tags at Elkhead Reservoir on 2 September 2024 and released. Tiger muskellunge were stocked in a protected cove with structure and vegetation. Short-term mortality (n = 2) was low as observed in the past.
- Northern Pike and Smallmouth Bass from the tournament have been delivered to be processed for tissue stable isotope comparisons with tiger muskellunge to understand diet overlap.
- Holdover tiger muskellunge will not be available in 2025 due to the necessary closure of the Wray Hatchery over winter for repairs.

Size-at-stocking (relevant in Elkhead Reservoir and others with high predator densities)

Relatively few systems have received tiger muskellunge as holdovers in Colorado. In addition, only two systems have received more than a single plant of holdover tiger muskellunge (Elkhead Reservoir and Harvey Gap Reservoir), and holdover tiger muskellunge stocking also coincides with stocking smaller, young-of-year tiger muskellunge, making it challenging to understand the interactions between holdover tiger muskellunge and smaller individuals generally stocked at higher densities. Without tagging of some sort or a more refined approach/design, the success of tiger muskellunge stocked at different sizes cannot be reliably differentiated from the data available. Thus, currently there is no definitive evidence that holdover tiger muskellunge outperform individuals stocked at smaller sizes in Colorado.

Tiger muskellunge are often challenging to capture/sample. This exacerbates obstacles related to comparing success between larger versus smaller stocked tiger muskellunge. Most systems in Colorado stocked with both holdover and smaller tiger muskellunge had very few or no individuals sampled during routine surveys following stocking. An example of this limitation is

Antero Reservoir that received 325 holdover tiger muskellunge (~475 mm) in 2017, but since 2016, over 8,000 smaller (~175 mm) tiger muskellunge were also stocked. In sampling efforts after these stocking events, six tiger muskellunge in total were observed, and because of overlap, their lengths/growth cannot be used to differentiate whether they were stocked at a larger or smaller size to evaluate differences in survival.

Generally, low catch rates of tiger muskellunge were observed throughout Colorado. Unfortunately, these observations, coupled with single events where large tiger muskellunge were stocked in close temporal proximity with small tiger muskellunge, make it challenging to quantify larger versus smaller tiger muskellunge survival. There are multiple examples of stocking holdover tiger muskellunge in the same year and/or the proceeding or following year as smaller tiger muskellunge, however, none of these examples provide definitive evidence that large tiger muskellunge perform differently than their smaller stocked counterparts. Each of the following figures is structured similarly to demonstrate overlap in stocking of large and small tiger muskellunge. In the figures, numbers of tiger muskellunge (TGM) stocked are represented with blue circles (large circles for holdovers and small circles for smaller tiger muskellunge) corresponding to the left, y-axis. Catch rates of tiger muskellunge are represented with open gray circles corresponding to the right, y-axis (note different units/gear in Harvey Gap Reservoir).



Lower Big Creek Reservoir received 135 holdovers (~575 mm) in 2005, but since 1990 over 15,000 smaller (~175 mm) tiger muskellunge were stocked. Stocked holdovers did not appear to increase catch rates, and tiger muskellunge caught following holdover stocking were caught across all size classes (i.e., not just sizes corresponding to the holdovers).



DeWeese Reservoir received 250 holdovers (\sim 325 mm) in 2016. Small tiger muskellunge were stocked across 3 decades (\sim 50,000 total). Catches from 2017-2019 were represented largely by tiger muskellunge > 600 mm, suggesting earlier plants of small fish contributed significantly to these elevated catches. Small fish and holdovers were not tagged and could not be differentiated.



Evergreen Reservoir received 145 holdovers (~575 mm) in 2005, but since 1989, ~5,000 smaller (~175 mm) fish were also stocked. Only one survey has been conducted since 2005, and two of three of tiger muskellunge captured were too large to be from the 2005 event. The third tiger muskellunge captured (~710 mm) could have come from stocking of either large or small tiger muskellunge. Capture rates of TGMs generally declined along with stocking.



Horseshoe Reservoir received 151 tiger muskellunge holdovers (~325) in 2016. Thousands of small (~175 mm) tiger muskellunge have been stocked since 1986, and tiger muskellunge catch rates were relatively high before holdover tiger muskellunge were stocked. Tiger muskellunge catch rates did increase when large tiger muskellunge were stocked, but thousands of small tiger muskellunge were stocked simultaneously, confounding interpretation/comparison.



Harvey Gap Reservoir has received the majority (~2,500 or ~50%) of all holdover tiger muskellunge ever stocked in Colorado. In the late 1990s small (~175 mm) tiger muskellunge were stocked, and later, larger, holdover tiger muskellunge were stocked. There is some evidence that higher tiger muskellunge catch rates were observed some years when holdovers were being stocked. Harvey Gap Reservoir contains many predators, and it may be possible that larger tiger

muskellunge have higher survival than smaller individuals in this particular system, but this has not been formerly tested, and requires tagged fish from both size classes to be stocked simultaneously.

Harvey Gap Reservoir is the only system in Colorado with relevant data where multiple plants of holdover tiger muskellunge have been stocked, with the exception of current work being conducted in Elkhead Reservoir. Additionally, smaller (~175 mm) tiger muskellunge were stocked in Harvey Gap Reservoir during a different time-period (over a decade earlier), and this allowed for a comparison of tiger muskellunge catch rates at different sizes. Catch rates of tiger muskellunge were higher (about double) during the time of holdover stocking at about 1/3 the density relative to periods when smaller tiger muskellunge were being stocked. However, these data are from a single system during different time periods and survival/catch rates may be different for reasons other than size-at-stocking (e.g., varying predator density, winter severity, growing degree days, etc. across years). Further, the tiger muskellunge survey data contain many gaps and zeros along with high variance, and it is likely that one tiger muskellunge captured in 2016 (860 mm) was from the stocking of small tiger muskellunge in the 1990s. Thus, differences in catch rates should be interpreted with caution. Despite these limitations, a simple one-tailed ttest assuming unequal variance was conducted to compare tiger muskellunge catch rates (routine boat electrofishing; tiger muskellunge caught per hour of electrofishing effort) when small fish were being stocked (1990s) in contrast with catch rates when holdover fish were being stocked (2014-2022) and significant differences were not detected (t-statistic = 0.96, p = 0.19). Thus, to better understand the relative performance of holdover versus smaller stocked tiger muskellunge, more simultaneous plants of tagged or marked fish must be conducted for comparison. Notably, Harvey Gap Reservoir, along with Elkhead Reservoir, have recently been stocked with small and holdover tiger muskellunge, and holdover fish in both systems have been tagged consistently for several years. In the future, this will allow for direct comparisons of survival between small tiger muskellunge and holdovers stocked in the same system at the same time.

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) 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 large predators like Northern Pike. Harvey Gap Reservoir has only received small tiger muskellunge a single year (2023) along with larger, tagged holdovers, and this action was not intended/designed for addressing research questions. Elkhead Reservoir has received simultaneous plants of tagged small and holdover tiger muskellunge in 2023, and 2024. However, these are early efforts, and few tiger muskellunge have been observed in Elkhead Reservoir where stocking densities are relatively low for small (~3-6/acre or 1-2.5/ha) and holdover (~0.3-0.8/acre or 0.1-0.3/ha) tiger muskellunge. Every other system in Colorado with data for interpreting tiger muskellunge holdover stocking success is represented by a single stocking event confounded by small tiger muskellunge stocking without tagging. Creating more opportunities to directly compare performance of small and holdover tiger muskellunge would help improve our understanding of the efficacy of tiger muskellunge as a management tool.

Tiger muskellunge interactions with Northern Pike

In addition to controlling undesirable prey fish species, tiger muskellunge have the potential to disadvantage/compete with undesirable predator species 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. In addition to Elkhead Reservoir, there were 24 lake/pond/reservoir systems in Colorado where tiger muskellunge had been stocked and where Northern Pike had been sampled at some point with any gear type through 2022. There are some data available for interpretation from these systems (Table 1).

Table 1. Northern Pike (NPK) total catch by system from 1980-2022. Overlap with tiger muskellunge (TGM) is indicated as "Yes" if Northern Pike were captured after tiger muskellunge were stocked, "Not observed after TGM" if Northern Pike were not encountered during surveys after tiger muskellunge stocking, or "No post-survey" if a survey was not conducted post-tiger muskellunge stocking. Northern Pike were being stocked actively in St. Vrain State Park Pelican and Milavec Reservoir.

System	NPK catch	Overlap w/ TGM?
Adobe Creek Reservoir	1	Not observed after TGM
Bear Creek Reservoir	1	Yes
Neenoshe Reservoir	1	Not observed after TGM
Pike View Reservoir	1	Not observed after TGM
Strontia Springs Reservoir	1	Not observed after TGM
Harriman Lake	2	Yes
John Martin Reservoir	2	Yes
Pueblo Reservoir	2	Not observed after TGM
Seeley Lake	2	Not observed after TGM
Wellington Reservoir #4	2	Yes
Queens Reservoir	3	Yes
Stalker Lake	3	Not observed after TGM
Cherry Creek Reservoir	4	Not observed after TGM
Lon Hagler Reservoir	10	Yes
Horseshoe Reservoir	16	Yes
Prewitt Reservoir	17	Yes
North Sterling Reservoir	18	Yes
Quail Lake	31	No post-survey
Lagerman Reservoir	35	Yes
Bonny Reservoir	49	Not observed after TGM
St. Vrain State Park Pelican	53	NPK stocked
Milavec Reservoir	104	NPK stocked
Sanchez Reservoir	412	No post-survey
Harvey Gap Reservoir	458	Yes
Elkhead Reservoir	4698	Yes

- In 13 of the 25 systems where Northern Pike were caught and tiger muskellunge were stocked, single digit (low) catches of Northern Pike were observed (note that the amount and types of effort vary across systems). In 8 of these 13 systems, Northern Pike were not observed after tiger muskellunge.
- In 7 of these 25 systems, 10-49 Northern Pike were sampled. These catch rates are still relatively low when compared to systems like Elkhead Reservoir where nearly 80% of the Northern Pike represented in Table 1 were caught.
- Of the remaining 5 systems in Table 1 there are 2 (St. Vrain State Park Pelican and Milavec Reservoir) were stocked with Northern Pike, 2 (Elkhead and Sanchez reservoirs) have only recently received tiger muskellunge, and Harvey Gap Reservoir has a longer history of tiger muskellunge stocking with some information available for interpretation.
- The following figure represents Harvey Gap Reservoir and presents the same data as the previous figure (tiger muskellunge stocking and catch rates through time), in addition to Northern Pike catch rates from routine boat electrofishing and gillnetting surveys. Boat electrofishing data suggest there may be some decline in Northern Pike catch rates (and variance) through time, but data were sparse, and these relationships were not supported statistically (i.e., linear regression). When considering gillnetting data, Northern Pike catch rates and variance were consistent and low.

Harvey Gap Reservoir tiger muskellunge (TGM) stocking events are represented with blue circles (large for holdovers and small for young-of-year tiger muskellunge) corresponding to the left, y-axis. Boat electrofishing catch rates of tiger muskellunge (open gray circles), and Northern Pike (filled gray circles) correspond to the right, y-axis. Northern Pike catch rates from gillnetting surveys are represented by filled black circles corresponding to the right y-axis in different units (number of Northern Pike sampled per overnight gill net set).

- The observation of differential catch rates of Northern Pike by gear prompted the consideration of the size of Northern Pike sampled with each gear. The mean length of Northern Pike sampled by boat electrofishing from 1990 to 2022 was ~400 mm compared to a ~650 mm mean length for Northern Pike sampled by gillnetting. Thus, if any decline in Northern Pike catch rates is observed during routine electrofishing surveys it is likely driven by a decline in small Northern Pike, while catch rates of larger Northern Pike during gillnetting surveys have remained low and consistent through time.
- Combined, anecdotal and relatively limited empirical data suggest that tiger muskellunge and Northern Pike overlap in few systems. Within these systems, Northern Pike appear to be caught more often where they were established prior to tiger muskellunge stocking. However, there are few systems with data and appropriate conditions available for comparison, and what systems are available (with the exception of Elkhead Reservoir) were not managed specifically to address research questions.
- To increase the potential for project success and address multiple questions simultaneously in a more controlled setting, assessment of the Northern Pike population in College Lake began in spring 2024 with the intent to stock tiger muskellunge to assess their interactions with Northern Pike. Using College Lake as a study site will allow for more controlled assessments of relative tiger muskellunge success based on size at stocking (small versus holdover), the presence of Northern Pike (tiger muskellunge predators/competitors), and stocking method (boat stocking in complex habitat versus introducing fish from shore directly from stocking trucks).
- 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 the group (over a dozen volunteers, CSU faculty, CSU students, Colorado Parks and Wildlife employees) sampled and Floy tagged ~400 Northern Pike to conduct a Schnabel population estimate indicating approximately 939 ± 208 (95% CI) catchable (> 300 mm) Northern Pike were present in College Lake. Animal Care protocols were completed and approved to ensure CSU faculty, staff, and student involvement.
- During course instruction at CSU, Dr. Myrick sampled (weighed and measured) multiple Northern Pike (with and without Floy tags applied during the spring 2024 Schnabel estimate) in mid-September 2024. These data will be shared, and can be used to further inform demographics of the Northern Pike in College Lake.
- Rigorously planning and evaluating Northern Pike responses to tiger muskellunge stocking in College Lake requires these baseline data collections. For example, tiger muskellunge stocking numbers of young-of-year fish are intended to match the catchable Northern Pike population in College Lake, and holdovers at 10% that number.

Overall project components

- All tiger muskellunge eye lenses collected in 2023 to gain a better understanding of layer development rates and thicknesses have been processed. These data coupled with stable isotope information will provide insight for interpreting information from tiger muskellunge eye lens tissue collected from the field in the future.
- Based on eye lens dissections in 2023, tiger muskellunge collected during 4 months of growth at the Wray Hatchery developed 4-7 eye lens layers. The cores of the eye lenses appeared to be relatively consistent near 400 to 500 microns. Full lens diameter measurements appear to be linearly related to tiger muskellunge lengths, similar to what is expected when comparing fish length and otolith development (see figure below).

Tiger muskellunge eye lens diameter as a function of length by sampling month were linearly related under the conditions within this study. Tiger muskellunge from a Nebraska source are represented by circles filled with similar shades of gray. Tiger muskellunge from a Pennsylvania source (PA) are represented by dark gray squares and were raised under different conditions due to differential timing of arrival at the Wray Hatchery. When available, data from both left (measured by J. Lepak) and right (measured by D. Williams) eye lens diameters from individuals are plotted for Month 1 (n = 12), and Months 2-4 (n = 9 for each sampling period).

- Collaboration continues to assess 56 reservoirs (of the 118 stocked with tiger muskellunge in Colorado from 1983 to 2024) where survey data are available to characterize responses of undesirable fish species to a variety of different tiger muskellunge stocking approaches.
- Current efforts with these data are focused on classifying the intensity of system-specific periods of tiger muskellunge stocking.

REFERENCES

Barndt, S., and J. Stone. 2003. Infestation of *Salmincola californiensis* (Copepoda: Lernaeopodidae) in wild Coho Salmon, Steelhead, and Coastal Cutthroat Trout juveniles in a small Columbia River tributary. Transactions of the American Fisheries Society 132:1027-1032.

Hoffman, G. L. 1999. Parasites of North American freshwater fishes. Second Edition. Comstock Publishing Associates, Ithaca, New York.

Lepak, J. M., C. N. Cathcart, and W. L. Stacy. 2014. Tiger muskellunge predation upon stocked sport fish intended for recreational fisheries. Lake and Reservoir Management 30:250-257.

Lepak, J. M., E. R. Fetherman, W. M. Pate, C. D. Craft, and E. I. Gardunio. 2012. An experimental approach to determine esocid prey preference in replicated pond systems. Lake and Reservoir Management 28:224-231.

RESEARCH PRIORITY:Food webs and predator-prey interactions (Part 1):
Rainbow Smelt Osmerus mordax – Walleye interactions 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.

MANUSCRIPT SUBMISSION

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. *In press*. Four decades of change: cyclical multi-trophic level responses to an introduced forage fish. Fisheries.

FULL MANUSCRIPT

1	Cyclical, multi-trophic-level responses to a volatile, introduced forage fish: learning from four
2	decades of food web observation to inform management
3	
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15 ABSTRACT

Species introductions can have significant effects on recipient ecosystems. Anticipating 16 potential ecosystem change in response to introduced species based on historical information can 17 help managers prepare for future conditions. Rainbow Smelt Osmerus mordax have been 18 introduced widely to improve sport fish growth. As intended, Walleye Sander vitreus growth in 19 20 Horsetooth Reservoir, Colorado increased after Rainbow Smelt introduction, but poor Walleye recruitment occurred as well. Additionally, opossum shrimp Mysis diluviana became absent from 21 both predator diets and intermittent surveys, the dominant *Daphnia* species in Horsetooth 22 23 Reservoir shifted and *Daphnia* densities declined significantly. These patterns were repeated during two different time periods of increased Rainbow Smelt abundance, suggesting that 24 Rainbow Smelt have a strong influence on multiple components of the ecosystem. The repetition 25 of responses to Rainbow Smelt offered the opportunity to evaluate indicators to anticipate 26 potential ecosystem regime shifts that restructure predator-prey dynamics across trophic levels. 27 Three predictors (i.e. high estimated Rainbow Smelt abundance, high catch rates of large 28 Walleye, and low *Daphnia* densities) were associated with poor Walleye recruitment. Simple 29 indicators like these could inform timely management decisions to take advantage of the benefits 30 31 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 32 Walleye; increasing availability or quality of Walleye spawning habitat; allowing more 33 34 protective or liberalized adult Walleye harvest to promote natural recruitment; and limiting Rainbow Smelt access to their spawning habitat. 35

36

37
38 INTRODUCTION

Understanding and anticipating ecological responses to species introductions is crucial, and 39 requires predictive techniques to forecast the potential impacts of invasive species (Dick et al. 40 2014). There are many examples of predictive models to determine habitat and system suitability 41 for invaders, and where they are likely to spread and establish (e.g. Fournier et al. 2019). 42 However, predicting the deleterious ecological impacts of invasive species establishment and 43 proliferation is less common, especially in aquatic environments (Ricciardi 2003). Because of the 44 importance of predicting invasive species impacts and anticipating the need for potential 45 46 management change, Ricciardi (2003) suggested that using empirical data offers opportunity to predict and anticipate potential ecological change from species invasions and proliferation. 47 Additionally, this suggestion was made within the context of empirical data that may lack 48 precision or comprehensiveness, as crude predictions can be informative, and refined further as 49 more contemporary and comprehensive data are collected (Ricciardi 2003). 50 Rainbow Smelt Osmerus mordax are an important forage species for a variety of sport fish 51 (Scott and Crossman 1973). Because of their desirable characteristics, Rainbow Smelt 52 introduction has been used as a management tool to enhance fisheries and encourage sport fish 53 54 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-55 Silva et al. 2006). 56 57 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. 58

59 2007). In some cases Rainbow Smelt are capable of controlling populations of invertebrate prey

60 species like opossum shrimp *Mysis diluviana* (Johnson and Goettl 1999). Further, Galbraith

61	(1967) found that when Rainbow Smelt and Fathead Minnow Pimephales promelas were
62	established in Sporley Lake (Michigan), Daphnia pulex were extirpated and replaced by smaller
63	D. galeata mendotae and D. retrocurva, similar to observations by Reif and Tappa (1966) in
64	Harvey's Lake, Pennsylvania. Rainbow Smelt also consume and compete with some coregonine
65	species (Loftus and Hulsman 1986; Evans and Waring 1987; Hrabik et al. 1998).
66	Declines in Walleye recruitment and abundance have been associated with increasing
67	Rainbow Smelt abundance (Schneider and Leach 1977; Johnson and Goettl 1999; Mercado-Silva
68	et al. 2007) which may be a result of predation on (Lepak et al. 2023) and competition with
69	young Walleye for prey resources (Johnson and Goettl 1999; Mercado-Silva et al. 2007; Lawson
70	and Carpenter 2014). Further, Rainbow Smelt populations have the potential to exhibit self-
71	regulated, cyclical patterns and alternating year-class dominance, attributable in part to their
72	cannibalistic behavior (Hendersen and Nepszy 1989; He and LaBar 1994). Thus, by exhibiting
73	strong interactions across multiple trophic levels from the "middle-out" (DeVries and Stein
74	1992; also see Stein et al. 1995 for an example involving Gizzard Shad, Dorosoma cepedianum),
75	Rainbow Smelt are a fundamental component of many food webs.
76	In 1983, Rainbow Smelt were introduced into Horsetooth Reservoir, Larimer County,
77	Colorado to enhance Walleye and Smallmouth Bass Micropterus dolomieu growth (Goettl and
78	Jones 1984). Historically, Horsetooth Reservoir was managed as a two-tiered fishery with
79	naturally reproducing Walleye (rare in Colorado reservoirs) as a primary component along with
80	stocked Rainbow Trout Oncorhynchus mykiss and landlocked Sockeye Salmon O. nerka (often
81	called kokanee salmon). The unique, naturally recruiting Walleye had been sustained largely on
82	a forage base of Yellow Perch Perca flavescens which collapsed, and managers attempted to
83	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. 84 Because of the importance of the Walleye fishery and reliance on a volatile Rainbow Smelt 85 population, Horsetooth Reservoir is a relatively data rich system with intermittent research and 86 monitoring efforts focused on multiple ecosystem components. Over 40 years of data are 87 available from this system, along with cyclical periods of high densities of Rainbow Smelt 88 89 during 1987–1996 and since 2013, provided an opportunity to evaluate long-term, multi-trophic level responses to Rainbow Smelt abundance across two distinct periods. In this paper, we 90 characterize community-level trophic interactions and population dynamics among Rainbow 91 92 Smelt and other biota including Walleye, M. diluviana, and Daphnia spp. We used machine learning to identify the best predictors of poor Walleye recruitment based on information from 93 historic and contemporary datasets spanning four decades. Repeated patterns in several 94 ecosystem components along with empirical observations prompted us to hypothesize that 95 indicators linked to Rainbow Smelt abundance would be the best predictors of poor Walleye 96 recruitment. We hoped to identify indices that can inform and prepare fisheries managers for 97 near-term impacts from Rainbow Smelt population dynamics in anticipation of taking actions 98 such as stocking Walleye fry or fingerlings, increasing availability or quality of Walleye 99 spawning habitat, altering Walleye harvest regulations, and limiting Rainbow Smelt access to 100 their spawning habitat. 101

102 Site and Historical Fisheries Management Description

Horsetooth Reservoir is a 755 ha impoundment at an elevation of 1655 m when full (capacity of ~200 million m³). The reservoir has three distinct basins, is relatively long (~11 km) and thin (~1 km) with a mean depth of 25 m and a maximum depth of 70 m (Figure 1). It was completed in 1949, and inflow mainly comes through the 13-mile-long Hansen Feeder Canal from the 107 Colorado-Big Thompson water diversion project.

Following Rainbow Smelt introduction into Horsetooth Reservoir in 1983, Walleye growth 108 increased through 1988 (Jones et al. 1994). Walleye had been reproducing naturally in 109 Horsetooth Reservoir, however, by 1990 Walleye recruitment had precipitously declined. In 110 response, ~5 and ~6 million Walleye fry (~6-7 mm TL) were stocked in mid-April of 1992 and 111 1993, respectively. Since these stocking efforts appeared unsuccessful, between ~50,000 and 112 ~88,000 Walleye fingerlings (~61 to 79 mm TL) were stocked annually during July–September 113 1994–1997. Walleye recruits were subsequently observed in higher numbers and Rainbow Smelt 114 115 abundance declined. No additional Walleye stocking occurred for the next 22 years (1998–2020). However, in an attempt to offset poor recruitment observed after Rainbow Smelt abundance 116 increased a second time, 3.6 million Walleye fry (~6 mm TL) were stocked annually during early 117 to mid-April 2021–2023. 118 While *M. diluviana* (opossum shrimp) can enter Horsetooth Reservoir through the Hansen 119 Feeder Canal, they were stocked in the reservoir from 1971 to 1974 to enhance the forage base 120 for salmonids (Nesler 1986). In the 1980s *M. diluviana* represented a major prey item for some 121 fish (Nesler 1986), but were not observed in the reservoir during sampling or in fish stomachs 122 123 during the two periods when Rainbow Smelt abundance was relatively high: from 1988–2003 and 2010–2015 (Jones 1985a, Johnson and Goettl 1999, Silver et al. 2021). 124 Despite M. diluviana being introduced to enhance salmonid forage, Horsetooth Reservoir 125 126 does not sustain salmonid natural reproduction, likely due to limited spawning habitat and whirling disease. Therefore, ~350,000 kokanee salmon fry were stocked annually as well as 127 ~40,000 catchable (> 150 mm TL) and 225,000 sub-catchable (< 150 mm TL) Rainbow Trout 128 129 were stocked prior to 2000 to sustain a sport fishery. After 2000, kokanee salmon stocking was

ended, and Rainbow Trout stocking was reduced to an average of ~13,000 catchable trout and
22,000 sub-catchable trout annually. Additionally, based on previous research in Colorado
reservoirs, it is likely that adult Walleye consume most of the stocked Rainbow Trout (Lepak et
al. 2012; Stacy and Lepak 2012). However, little information is available on salmonid
distribution and abundance in Horsetooth Reservoir, since routine sampling surveys were
designed to capture Walleye and other non-salmonid sport fish.

Horsetooth Reservoir fluctuates significantly (on the order of 10-30 m annually; see 136 Supplemental Information; Figure S1) since it is used as a municipal and agricultural water 137 138 source and for providing water for irrigation/agriculture. This limits the littoral habitat available for aquatic organisms. For example, at the end of 2000, the reservoir was drawn down 139 substantially to < 5% (~8 million m³) capacity for maintenance, and at times during the winter 140 was over 40 meters below full pool (Northern Colorado Water Conservancy District). In the 141 early spring of 2001–2003, Horsetooth Reservoir was at < 10% capacity, limiting Rainbow 142 Smelt and Walleye access to known spawning habitat in the reservoir inlet. However, there were 143 indications that Rainbow Smelt had declined in the years leading up to the drawdown (Johnson 144 and Goettl et al. 1999) and their decline continued through 2010. After 2010, the Rainbow Smelt 145 146 population increased again, and the pattern of low Walleye recruitment, low M. diluviana density, and low Daphnia density, and dominance by D. galeata was repeated. 147

148 MATERIALS AND METHODS

149 Walleye Diet and Stable Isotope Analyses

150 Gillnetting in late April through May and boat electrofishing in July and August surveys are

done intermittently in Horsetooth Reservoir (see more detail in Walleye Recruitment and

Abundance Indices section below). Individual Walleye were retained from these sampling eventsto examine diet and growth.

Walleye diets from 1983-1992 and 1994-1996 were based on stomach contents of collected 154 fish. Stomach contents were removed and analyzed under a dissecting microscope to identify 155 each prey item to taxon, and mean percent volume was calculated for each prey item to obtain a 156 snapshot of what fish had recently eaten (Jones 1985a) based on stomach contents. In 2008, 157 carbon and nitrogen stable isotope values of Walleye and their prey were used to obtain a time-158 integrated estimate of diet (Post 2002; Johnson et al. 2015). These data were analyzed using 159 160 Bayesian mixing models. In 2013 and 2017–2019, these data were analyzed with a model written in R that is designed to solve mixing equations for stable isotopic data within a Bayesian 161 framework (SIMMR 0.4.5; Parnell 2021). Trophic fractionation (i.e. differences in carbon and 162 nitrogen stable isotopes between prey and predator) and error for δ^{13} C (0.4 and 1.3, respectively) 163 and $\delta^{15}N$ (3.4 and 1.0) were set to values established by Post (2002). Values for burn-in (1,000 164 separate simulations) and the number of iterations (each simulation run 10,000 times) were the 165 SIMMR default settings, and additional iterations were unnecessary since Gelma-Rubin 166 convergence diagnostics never exceeded 1.01 for any model. 167 168 In 2013, 30 Walleye were collected for analyses. Prey species targeted for collection had to be

abundant, of edible size, and common in Walleye diets in the past. These prey items were
collected opportunistically in Horsetooth Reservoir using beach seines, various nets, minnow
trapping, and boat electrofishing. Prey items included in analyses were Rainbow Smelt (*n*=4), *Decapoda* (*n*=6), hatchery-reared Rainbow Trout (*n*=9), dipterans (*n*=5 composite monthly
samples of multiple individuals collected from May to October), large zooplankton (*n*=3
composite samples of multiple individuals representing bulk zooplankton collected with a 500

175	micron mesh net in June, July, and September), Gizzard Shad $(n=3)$, and Yellow Perch $(n=3)$.
176	Prey items were placed into the following categories: Rainbow Smelt, Decapoda (crayfish),
177	salmonidae (Rainbow Trout), other invertebrates (dipterans and zooplankton), and other fish
178	(Gizzard Shad and Yellow Perch).
179	In 2017, 2018, and 2019, 42, 14, and 42 Walleye were collected for analysis, respectively.
180	During these years, prey species targeted for collection had to be abundant, of edible size, and
181	common in Walleye diets in the past. Cursory diet analyses, indicated that Walleye were mainly
182	focused on consuming Rainbow Smelt. Thus, Rainbow Smelt were targeted with fine mesh gill
183	nets all three years, and other prey species were collected opportunistically with netting,
184	trapping, and boat electrofishing efforts. Prey items collected for analyses were Rainbow Smelt
185	($n=213$ across all three years), <i>Decapoda</i> ($n=6$), large zooplankton ($n=6$ composite samples of
186	multiple individuals representing bulk zooplankton collected monthly with a 500-micron mesh
187	from net from June through November 2019 with values averaged across samples from each of
188	the three reservoir basins), and Gizzard Shad ($n=36$ from 2017 and 2018). These prey items were
189	placed into the following categories: Rainbow Smelt, Decapoda, other invertebrates
190	(zooplankton), and other fish (Gizzard Shad). Because samples from 2017-2019 were collected
191	during a relatively short time window, and values for Rainbow Smelt stayed relatively consistent
192	during this time, prey items from all three years were used for mixture modeling of Walleye.
193	Stable isotope values were measured using a Thermo Delta V isotope ratio mass spectrometer
194	(IRMS) interfaced to a NC2500 elemental analyzer at the Cornell Isotope Laboratory (Ithaca,
195	New York, USA). In-house standards were analyzed every 10 samples to ensure precision and
196	accuracy. The overall standard deviation of these samples fell below 0.20‰ for $\delta^{13}C$ and $\delta^{15}N$. A
197	methionine standard was used to quantify the ability of the instrument of measure across a

198 gradient of amplitude intensities. Values for δ^{13} C and δ^{15} N were corrected using primary 199 references of Vienna Pee Dee Belemnite (a Cretaceous marine fossil, *Belemnitella americana*, 200 from the Pee Dee Formation in South Carolina used as a standard for carbon-13), and 201 atmospheric air. To avoid potential bias from differing lipid concentrations among samples and 202 species, corrections for lipid content from Post et al. (2007) were applied to δ^{13} C values:

203

$$\delta^{13}C_{normailzed} = \delta^{13}C_{measured} - 3.32 + 0.99 \text{ x C:N}$$

where C:N is the carbon-to-nitrogen ratio.

206 Rainbow Smelt Diet and Stable Isotope Analyses

Rainbow Smelt were collected using fine and large mesh gill nets, trawls, boat electrofishing, 207 and beach seines throughout the study period. Rainbow Smelt diets were analyzed using stomach 208 contents of fish collected in 1984 (Jones 1985a), 1987 (Thomas 1989), 1989 to 1992 (Goettl 209 1990, 1991, 1992, 1993), 1994 (Goettl and Johnson 1995) and 1995 (Goettl and Johnson 1996), 210 or stable carbon and nitrogen isotope values of predator and prey coupled with a Bayesian 211 212 mixing model (SIMMR 0.4.5) for samples collected during 2017-2019. For both volumetric diet composition and stable carbon and nitrogen isotope analyses, Rainbow Smelt prev were grouped 213 into four categories: M. diluviana, Rainbow Smelt, zooplankton (e.g. daphnids, copepods), and 214 other invertebrate prey (e.g. dipterans, amphipods). 215 For stomach content analyses, Rainbow Smelt ≥ 100 mm TL were commonly analyzed 216

separately due to their potential to consume *M. diluviana*, Walleye larvae, and smaller Rainbow

- Smelt. In 1984, 1987, 1989, and 1991, only data from Rainbow Smelt \geq 100 mm TL were used.
- In 1984, two size classes of 100–150 mm TL (n=3) and > 150 mm TL (n=2) were considered. In
- 220 1987, three size classes of 100–125 mm TL (*n*=16), >125–150 mm TL (*n*=21), and > 150 mm

TL (n=51) were used. Diet composition was weighted by sample sizes within each respective size class. In 1989, all Rainbow Smelt > 100 mm TL (n=90) were used together, and the same was done in 1991 (n=99). In 1990, 1992, 1994, and 1995, data were collected from Rainbow Smelt sampled of all sizes (n=94, 212, 435, and 131, respectively). Stomach contents were removed and examined under a dissecting microscope, identified to taxon, and quantified as mean percent volume by prey item (Jones 1985a).

For stable isotope analyses in 2017-2019, we classified Rainbow Smelt as either predators (\geq 227 130 mm TL) or prey (< 130 mm TL) since we noted a change in isotope values, which indicated 228 a diet shift, when Rainbow Smelt reached 130 mm TL. There were 20, 9, and 73 Rainbow Smelt 229 ≥130 mm TL in 2017, 2018, and 2019 samples, respectively. Other items measured and included 230 in the stable isotope mixing models were zooplankton (as described in the Walleye diet analysis), 231 and dipterans, which were regularly found in Rainbow Smelt stomachs, but not collected during 232 these years. Thus, we included data from dipterans collected in 2013 (described in the Walleye 233 diet analysis) despite disparate collection time periods. In 2019, we collected Rainbow Smelt 234 (n=500) using a special effort using suspended fine mesh gillnets from May to November. All 235 stomach contents from these fish were inspected for the presence of *M. diluviana* and larval and 236 237 juvenile Walleye. In all cases (volumetric diet composition and composition established with stable carbon and nitrogen isotope analyses) Rainbow Smelt prey categories were collapsed into; 238 M. diluviana, Rainbow Smelt, zooplankton (e.g. daphnids, copepods), and other invertebrate 239 240 prey (e.g. dipterans, amphipods).

241 Walleye Recruitment and Abundance Indices

Gillnetting (late April–May) surveys have occurred most years beginning in 1983 during May
in Horsetooth Reservoir (Jones et al. 1994). Generally, a set of 20 standardized monofilament

244 gill nets are used to assess the adult Walleve population. Nets are ~ 46 m long and ~ 1.8 m in depth, with 6 graduated panels ranging from 13–76 mm bar-mesh increasing in 6–13 mm 245 increments and set overnight in the same location perpendicular shore. Net soak times were often 246 estimated to the nearest hour, reported to the nearest minute, or reported as "overnight", which 247 limited us to using this metric ("overnight") when combining these data. Thus, Walleye catch per 248 unit effort (CPUE) during spring gillnetting surveys was expressed as Walleye catch per 249 overnight net set. Catches from each of the 20 nets combined were used to calculate CPUE for 250 that year. To remain consistent with previous research efforts (e.g. Johnson and Goettl 1999), 251 252 two different size classes of Walleye were used to characterize the population by representing reproductive adult Walleye and juvenile Walleye recruiting to the sampling gear: 150–300 mm 253 TL (predominately age-1 Walleye recruits based on our unpublished data), and \geq 451 mm TL 254 255 (predominantly adult reproductive Walleye). While it would have been preferable to also assess young-of-the-year Walleye, the gill net mesh size used was too large to do this. Therefore, we 256 opted to use the most consistent long-term source of Walleye catch data to develop indices and 257 predictors. 258

259 Walleye Growth

Historically, Walleye growth comparisons were standardized to mean TL at age-3 (Goettl and
Jones 1984, 1986), so we used this metric for the entire time-series. Walleye TL at age-3 in 1991

and earlier were back-calculated from scales collected in 1983 (n=204), 1984 (n=210), 1985

263 (n=94), 1986 (n=93), 1988 (n=68), 1989 (n=97), 1990 (n=138), 1991 (n=94), and 1992

264 (*n*=187) (Goettl and Jones 1984, 1986; Jones 1985b; Goettl and Thomas 1987; Goettl 1990,

1991, 1992, 1993). Walleye TL at age-3 in 2001 and later were back-calculated from sectioned

otoliths (Farrell et al. 2021) collected in 2012 (*n*=40), 2013 (*n*=119), 2019 (*n*=131), and 2021

267 (*n*=75). Mean Walleye length at age-3 from scales and otoliths were computed each year when \geq 268 2 individuals were represented. Standard error was calculated from 2001–2016, but only mean 269 ages were available for earlier data, and these were weighted by sample size to estimate yearling 270 means.

271 Rainbow Smelt Abundance Indices

When available hydroacoustic surveys were used to estimate Rainbow Smelt abundance. 272 During 1993–1996, surveys were conducted along longitudinal transects down the center of the 273 north-south axis using a BioSonics 420 kHz, dual-beam echosounder and analyzed using echo 274 275 integration with *in situ* trawl catch data to determine mean Rainbow Smelt body size and target strength (-50 dB; Johnson and Goettl 1999). Due to lower Rainbow Smelt abundance during 276 (1998–2013), (1998–2013) were conducted along longitudinal transects down the center of the 277 north-south axis, but with a 200 kHz Hydroacoustic Technology Incorporated Model 243 split 278 beam digital echosounder and real-time target tracking algorithm. Individual fish targets were 279 identified based on a minimum of four echoes, and target strengths corresponding to individuals 280 > 5 cm TL and < 20 cm TL were based on fine mesh gill net catches (our unpublished data) and 281 a target strength-length relationship for Rainbow Smelt (Rudstam et al. 2003). Rainbow Smelt 282 283 were largely observed near the thermocline and in the epilimnion during sampling based on hydroacoustics and vertical gillnetting. Targets below 30 m, which were usually fish > 20 cm 284 TL, were not used in analyses. During 2017–2023, surveys were conducted along zig-zag 285 286 transects down the center of the north-south axis of the reservoir with a 200 kHz Hydroacoustic Technology Incorporated Model 243 split beam digital echosounder (the same equipment as 287 288 1998–2013), and echo integration was used instead of target tracking to enumerate Rainbow 289 Smelt, and *in situ* target strengths were used to determine Rainbow Smelt density (Johnson and

Goettl 1999). We note that gear, personnel, and methodology were inconsistent between historic
and contemporary hydroacoustic surveys, but other data are unavailable from this system during
the time periods of interest.

Prior to initiation of hydroacoustics surveys in 1993 Rainbow Smelt abundance was 293 documented using midwater trawling surveys. Trawl surveys were conducted at night in a 294 stepped-oblique approach from the surface to a depth of 18 m using a net with a 6 x 6 m opening 295 and graduated mesh from 203 mm (stretch) at the open end to 13 mm at the cod end (Kirn and 296 LaBar 1991). The relationship between estimated Rainbow Smelt densities from these surveys 297 298 and hydroacoustic surveys in years these surveys overlapped are described in Johnson and Goettl (1999). We also used routine gillnetting (late April–May) and boat electrofishing in July–August 299 (Jones et al. 1994) to develop an annual index of Rainbow Smelt based on data from different 300 gears. The coarse index was represented by the total Rainbow Smelt catch across these surveys 301 divided by the number of surveys that occurred in a given year. This index was calculated 302 because we were interested whether Rainbow Smelt catches during surveys not designed to 303 target Rainbow Smelt would be still be able to identify times of high Rainbow Smelt abundance. 304 This approach would allow these surveys to replace hydroacoustic and fine mesh gill netting 305 306 sampling which would save time, effort, and money.

307 *Mysis diluviana* Density

Estimates of *M. diluviana* density (number m^{-2}) were obtained at 10 locations using a 1 m

diameter, 500 µm mesh net that was towed vertically through the water column at night in 1999,

2003–2006, 2008, 2012, 2013, 2015–2018, and 2020–2023 in strata representative

311 (proportionally by depth) of regions in Horsetooth Reservoir that support *M. diluviana*.

Specifically, strata included 10-20 m (n=1), >20-30 m (n=1), 30-40 m (n=4), 40-50 m (n=3),

and 50–60 m (*n*=1) depths depending on water conditions (Silver et al. 2021). Benthic trawl data
from 1981 were used to develop an early, conservative *M. diluviana* density estimate (Nesler
1986).

316 Daphnia Density and Dominant Species

Horsetooth Reservoir is similar to some other Colorado Reservoirs in that the highest 317 densities of zooplankton generally occur in surface waters (<10 m depth) (e.g. Nelson 1971; 318 Johson and Goettl 1999). During 1987–1993, macrozooplankton sampling in Horsetooth 319 Reservoir was conducted April-September in mid-morning with a metered Clarke-Bumpus net 320 fished in the top 5 m of the water column (Johnson and Goettl 1999). During 1994–1996, 2002– 321 2023, sampling was also conducted April-September in mid-mornings, but with a 153 µm 322 Wisconsin net fished in the top 5 m or 10 m of the water column. Sampling during these years 323 were done by either Colorado State University, the Bureau of Reclamation and Northern 324 Colorado Water Conservancy District, or Colorado Parks and Wildlife personnel. Since some 325 methodology changed over time, we used the sampling day from each year with the highest 326 estimated mean density of *Daphnia* (individuals L⁻¹) as an index of macrozooplankton 327 abundance. If sampling was done in more than one of the reservoir's three basins during the 328 329 same year, we averaged data from all basins sampled for each sampling day. We also calculated the percent of large-bodied *D. pulex/pulicaria* within each year's index sample. 330

331 Water Storage Index

Since low water levels can negatively influence access to both Rainbow Smelt and Walleye
spawning areas in Horsetooth Reservoir, water storage during spawning periods was considered
as a factor that could influence relationships between Walleye recruitment and Rainbow Smelt.
During the 2001–2003 drawdowns in Horsetooth Reservoir, limited access to known spawning

habitat for Rainbow Smelt and Walleye in the reservoir inlet was observed, but not thought to be
due to water level (K. Kehmeier, Colorado Parks and Wildlife, personal communication).
However, sampling, observation, and egg-take operations suggest Rainbow Smelt and Walleye
begin to spawn in late March. So, we calculated, using data provided by the Northern Colorado
Water Conservancy District, annual mean daily March water storage as an indicator of water
conditions.

342 Machine Learning Prediction

We compiled disparate abiotic and biotic data from Horsetooth Reservoir and developed 343 annual indices to evaluate their importance as predictors of Walleye recruitment failure/success. 344 We applied a machine learning approach (Random Forest; RF) to evaluate the importance and 345 performance of seven predictors of Walleye recruitment: 1) gill net catch rates of large (≥ 451 346 mm TL) Walleye (LWAL; Walleye overnight net⁻¹); 2) estimated number of Rainbow Smelt 347 from hydroacoustic surveys (SONAR); 3) Rainbow Smelt encountered during routine sampling 348 efforts (RSM; number survey⁻¹); 4) estimated *M. diluviana* density (MYSIS; *M. diluviana* m⁻²); 349 5) estimated peak *Daphnia* density (DAPHd; *Daphnia* L⁻¹); 6) the percent of peak *Daphnia* 350 sample composed of larger-bodied D. pulex/pulicaria (DAPHc; %); 7) reservoir water storage 351 (H2O; km³). A one-year offset was applied to the CPUE of Walleye 150–300 mm TL during 352 routine spring gillnetting to coincide with data collected the previous year when that cohort of 353 Walleye hatched (to reflect hatching conditions). Missing data were predicted using linear 354 355 interpolation (detailed methodology available in Supplemental Information; Linear Interpolation). 356

A machine learning approach was selected because many of the predictors were highlycorrelated and could have complex interactions that precluded the use of traditional statistical

359 approaches. Significant (p < 0.01) Pearson correlation coefficients (r) were found between LWAL and SONAR (r = 0.72). LWAL and MYSIS (r = -0.41); LWAL and DAPHd (r = -0.44); 360 and LWAL and DAPHc (r = -0.57); LWAL and H2O (r = 0.44); SONAR and MYSIS (r = -361 0.48); SONAR and DAPHd (r = -0.47); SONAR and DAPHc (r = -0.58); SONAR and H2O (r =362 0.43). To perform the RF analysis, we used the 'randomForest' package in R (R Development 363 Core Team 2011; version 4.2.2). Accuracy and error rate calculations for each observation using 364 out-of-bag predictions were based on 2,000 regression trees (i.e. predicting data withheld from 365 each tree). Data predictions that were not used to evaluate fit were considered a form of cross-366 367 validation. Variable importance was assessed by comparing the increase in mean squared prediction error and node purity associated with each individual covariate (Gini 1912; Liaw and 368 Wiener 2002; Cutler et al. 2007). Increases in mean square error reflected as increases in 369 Walleve recruitment estimate error, while increases in node purity was used to assess variable 370 importance. At each node split in a tree, there is a resulting decrease in the Gini index (a measure 371 of the discrepancy between observations and predictions; Gini 1912). The sum of these decreases 372 throughout the RF for a given variable, normalized by the number of trees was used as an 373 indicator of variable importance (node purity). Higher node purity indicated that a variable was 374 375 more important for Walleye recruitment prediction when compared to another. Based on results, we opted to develop partial dependence plots of Walleye 150-300 mm TL 376 CPUE as a function of the observed values for the three best predictors (SONAR, LWAL, and 377 378 DAPHd). This approach provides predictions associated with a predictor at observed points while averaging, and holding constant, the effects of other predictors to better visualize the effect 379 380 of the predictor of interest (pdp Package in R; Greenwell 2017). 381 RESULTS

382 Trophic and Predator-Prey Interactions

In 1984, the stomach of one 255 mm TL Walleye collected during the routine gill net survey 383 contained Rainbow Smelt (Jones 1985a). The presence of Rainbow Smelt in Walleye diets from 384 routine surveys increased thereafter, and were a significant component of Walleye diets from 385 1988–1996, along with invertebrates and salmonids (e.g. Rainbow Trout) which were stocked 386 more frequently prior to 2000 (Jones et al. 1994; Johnson and Goettl 1999). Walleye largely 387 consumed crayfish when Rainbow Smelt were less abundant (Johnson et al. 2015; K. Kehmeier, 388 Colorado Parks and Wildlife, personal communication) and salmonid stocking was reduced. This 389 390 information coupled with stable carbon and nitrogen isotope data in 2008, 2013, and 2017–2019, indicated that Walleye consumed a mix of prey sources in the reservoir in 2008, but transitioned 391 to primarily a Rainbow Smelt diet by 2017 (Figures 2, 3). Zooplankton were generally 5% or less 392 of Walleye diets during 2017-2019 based on the mixing model approach (Figures 2, 3). 393 When Rainbow Smelt were first introduced into Horsetooth Reservoir, M. diluviana 394 composed most of their diet. Mysis diluviana disappeared from Rainbow Smelt diets by 1988 395 (Johnson and Goettl 1999), and were replaced by *Daphnia* and dipterans as well as an increasing 396 occurrence of cannibalism in the 1990s after first being recorded in 1987 (Figure 4). Only 397 398 zooplankton were observed in Rainbow Smelt diets in 1994 and 1995 (Goettl and Johnson 1995; Goettl and Johnson 1996), but in 2017–2019, stable carbon and nitrogen values indicated that 399 Rainbow Smelt \geq 130 mm TL were getting large portions of their energy from cannibalism 400 401 (Figures 3, 4). During more contemporary stable isotope analyses, *M. diluviana* were not readily available for collection, so they could not be included in the SIMMR analyses. Further, no M. 402 diluviana or larval Walleye were observed in 500 Rainbow Smelt stomachs from fish collected 403 404 across seasons in 2019 from May to November, and most prey biomass was Rainbow Smelt.

405 Analyses of mtDNA from stomach contents of Rainbow Smelt collected near the inlet of

406 Horsetooth Reservoir in 2022 indicated they were consuming some Walleye eggs or larva

407 (Lepak et al. 2023). Rainbow Smelt diets linked them to organisms within multiple trophic levels

408 from the middle-out, corroborating previous findings and allowing for development of a

409 predictive framework (DeVries and Stein 1992; Stein et al. 1995; Johnson and Goettl 1999).

410 Walleye Recruitment and Abundance Indices

Based on standardized gill net catches, Walleye 150-300 mm TL were rarely encountered 411 during periods of relatively high Rainbow Smelt abundance. Catch rates of these small Walleye 412 were generally below 0.5 fish net⁻¹ during these periods, indicating poor recruitment (Figure 5A). 413 Concomitant with Walleye fingerling stocking during 1994–1997 to supplement natural 414 reproduction, Rainbow Smelt abundance declined and catch rates of Walleye 150-300 mm TL 415 increased to > 0.5 fish net⁻¹ (Figure 5A). Catch rates occasionally approached or exceeded 2.0 416 fish net⁻¹ until 2012, when the Rainbow Smelt population rebounded and catch rates of small 417 Walleye declined again (Figure 5A). 418 Catch rates (fish net⁻¹) of large Walleye (≥ 451 mm) in standardized gill net samples showed 419 increases during periods of elevated Rainbow Smelt abundance (Figure 5B). The pattern of 420

421 increasing catches of large Walleye was observed in the 1990s when Rainbow Smelt were

422 abundant (Johnson and Goettl 1999), and then again beginning around 2010. This repetition was

423 expected, as consumption of Rainbow Smelt forage previously produced relatively large Walleye

424 in Horsetooth Reservoir (Jones et al. 1994; Johnson and Goettl 1999), and likely increased the

425 number of large fish available for capture.

426 Walleye Growth

427 Walleye growth responded positively to increases in Rainbow Smelt abundance in the late 1980s to mid-1990s (Figure 5C). Walleye growth after the introduction of Rainbow Smelt 428 appeared to remain high (an increase in length by 50% at age-3) compared to observations prior 429 to Rainbow Smelt introduction (Jones et al. 1994). Notably, poor Walleye recruitment created 430 large cohort gaps (e.g. periods after 1989 and 2013) and few Walleye were captured from 431 cohorts following the first Rainbow Smelt population increase and leading up to the second 432 (Figure 5). These gaps and low sample sizes are informative because they indicate large declines 433 in Walleye recruitment and year class failure lagging approximately 5 years after Rainbow Smelt 434 435 abundance increased.

436 Rainbow Smelt Abundance Indices

Hydroacoustic and trawl surveys indicated there were millions of Rainbow Smelt soon after 437 their introduction in Horsetooth Reservoir through the mid-1990s (Figure 5D). Rainbow Smelt 438 estimates peaked at almost ten million individuals in 1994 during this initial expansion period, 439 but declined by 2000 to the third and first lowest Rainbow Smelt hydroacoustic estimates two 440 and three years, respectively, before drawdowns. After Horsetooth Reservoir was drawn down 441 during 2001–2003, Rainbow Smelt were not observed in samples until 2010, when a single 442 Rainbow Smelt was captured during a gill net survey. Based on hydroacoustic data, Rainbow 443 Smelt abundance began increasing again after 2010, and by 2018 they achieved numbers similar 444 to those observed during their first expansion. Rainbow Smelt catches during routine spring and 445 446 summer surveys also indicated there were two pulses of increased abundance (Figure 5E).

447 *Mysis diluviana* Density

Mysis diluviana presence in Horsetooth Reservoir was first confirmed in 1981 from benthic
trawl catches (Nesler 1986). The presence of *M. diluviana* was also apparent in fish diets (e.g.

450Rainbow Smelt $\geq 100 \text{ mm TL}$) until 1988 (Jones 1985a; Thomas 1989). Subsequently, very few451*M. diluviana* were captured until after the 2004 drawdown and refilling of Horsetooth Reservoir.452For the next 10 years, during a period of relatively low Rainbow Smelt abundance, *M. diluviana*453appeared more frequently during sampling, and surveys indicated their abundance had increased454relative to observations around 2000 (Figure 5F). However, *M. diluviana* dropped below455detection limits again by 2020 following the resurgence of Rainbow Smelt abundance.

456 Daphnia Density and Dominant Species

457 Peak density of *Daphnia* did not exceed 10 individuals L⁻¹ during 1989–1994. During this

458 period, small-bodied D. galeata mendotae was the dominant species. This pattern of low

459 Daphnia L⁻¹ dominated by D. galeata mendotae occurred again in Horsetooth Reservoir during

460 2012–2023 (Figure 5G). Both these time periods corresponded to relatively high Rainbow Smelt

461 abundance. *Daphnia pulex/pulicaria* are generally considered more desirable prey items because

they tend to be larger than *D. galeata mendotae*. Thus, it appears that when Rainbow Smelt

463 abundance is high, *Daphnia* abundance and species composition changes as described here and

464 previously during 1989–1994 (Johnson and Goettl 1999). In contrast, when Rainbow Smelt

abundance is relatively low, higher densities of *Daphnia* (≥ 10 individuals L⁻¹) usually

466 dominated by *D. pulex/pulicaria* are observed (Figure 5G).

467 Water Storage Index

468 Horsetooth Reservoir water storage fluctuated significantly over the course of the study

469 (Supplemental Information; Figure S1). During 2001–2003, the reservoir was drawn down

- 470 significantly during Rainbow Smelt and Walleye spawning periods (Figure 5H). Rainbow Smelt
- 471 had already shown signs of decline prior to this drawdown in 1998 and 1999 (Figure 5D).

472 Walleye recruitment indices following the drawdown remained relatively high for several years,

473 while Rainbow Smelt abundance indices remained low (Figure 5A, D).

474 Machine Learning Prediction

Rainbow Smelt abundance estimates from hydroacoustic surveys (SONAR), the number of 475 large Walleye captured during routine spring gill net surveys (LWAL), and peak density of 476 Daphnia (DAPHd), were the three most important predictors of the Walleye recruitment index. 477 These three predictors had higher importance metrics compared to the other four predictors 478 examined (Figure 6). Overall, the RF approach performed relatively well with a mean square of 479 residuals equal to 0.39 and explaining 55% of variance in the observed data (Figure 5A). Typical 480 of RF, the model tended to over predict low Walleye recruitment index values and under predict 481 high values (Figure 7). Based on partial dependence plots, we found that poor Walleye 482 recruitment was correlated with Rainbow Smelt abundance estimates greater than 3 million 483 (Figure 8A), large Walleye catch rates greater than 1 fish net⁻¹ (Figure 8B), and *Daphnia* 484 densities less than 10 individuals L⁻¹; (Figure 8C). Conversely, high Walleye recruitment was 485 correlated with Rainbow Smelt abundance estimates less than 3 million, large Walleye catch 486 rates greater than 1 fish net⁻¹, and *Daphnia* densities of at least 10 individuals L⁻¹. 487

488 DISCUSSION

Predicting deleterious impacts from invasive species to anticipate potential ecological change is important from a management perspective. For example, extensive planning and resources may be necessary to respond to the introduction and establishment of invasive species (e.g. Dreissenid mussels in the Great Lakes region; Nalepa and Schloesser 2013). Thus, forecasting ecological change before it occurs allows for time and resource allocation to prepare for and respond to undesirable ecological and economic impacts from invasive species. Predicting poor 495 recruitment failure is of particular importance to Horsetooth Reservoir managers because Walleye eggs are not regularly collected and propagated for stocking when Walleye are 496 reproducing naturally (K. Kehmeier, Colorado Parks and Wildlife, personal communication). If 497 indicators the previous year suggest that recruitment of Walleye the following spring will be 498 limited, actions can be taken to collect and raise Walleye eggs to the fry or fingerling stage for 499 stocking. Allocating resources and preparing for egg collection and propagation is one 500 management response to poor Walleye recruitment. However, managers may also consider other 501 actions like increasing or improving Walleye spawning habitat (which could require reservoir 502 503 operation changes), altering harvest regulations to protect spawning adult Walleye, encouraging harvest of large Walleye when they cannibalize sub-legal juveniles, or limiting Rainbow Smelt 504 access to their spawning habitat (i.e. blocking the reservoir inlet during spawning) to reduce their 505 506 abundance. All of these actions require resources and forethought to plan and implement. Thus, anticipating ecological change can be important for balancing valuable fisheries and 507 management actions in the context of invasive species and their deleterious impacts. 508 Rainbow Smelt exhibited strong middle-out influence on the Horsetooth Reservoir food web 509 since their introduction in 1983. Significant responses by organisms at trophic levels above and 510 511 below Rainbow Smelt were noted when the Rainbow Smelt population increased, and reciprocal observations were made when the population declined (Jones et al. 1994; Johnson and Goettl 512 1999). We observed the influence of increasing Rainbow Smelt abundance on Horsetooth 513 514 Reservoir biota during two separate time periods, providing an opportunity to evaluate biotic responses iteratively to corroborate initial observations. Our observations demonstrated that 515 Walleye, M. diluviana, and Daphnia exhibited repeated responses to high Rainbow Smelt 516

abundance, suggesting Rainbow Smelt play a dominant role in driving food web interactions and
population dynamics across trophic levels in Horsetooth Reservoir.

Rainbow Smelt have been associated with Walleye recruitment failure in other systems 519 (Evans and Loftus 1987; Mercado-Silva et al. 2007). This undesirable outcome also occurred in 520 Horsetooth Reservoir, and Walleye recruitment essentially ceased when Rainbow Smelt 521 abundance was high (Johnson and Goettl 1999). Thus, high Rainbow Smelt abundance appears 522 to improve Walleye growth, but comes at the expense of Walleye recruitment. Rainbow Smelt 523 consumption of larval Walleye near the inlet of Horsetooth Reservoir was observed (Lepak et al. 524 525 2023) and is likely reducing Walleye recruitment directly. However, this finding does not discount other potential causes of poor recruitment. For example, the presence of relatively high 526 densities of large Walleye (LWAL) coincided with periods of poor Walleye recruitment, and this 527 could be attributed to cannibalism or competition among high densities of larvae, creating a 528 Ricker-type stock-recruitment relationship (Ricker 1954). However, despite observations of 529 Walleye cannibalism in other systems (e.g. Forney 1980; Hansen et al. 1998) information on 530 piscivory by Horsetooth Reservoir Walleye indicates they focused largely on Rainbow Smelt 531 when they were abundant based on diet information. Conversely, when Walleye larvae are likely 532 533 at their lowest density (during periods of poor recruitment), Rainbow Smelt are likely available in high densities as alternative Walleye forage. Therefore it appears that Walleye cannibalism is 534 a less important driver of poor Walleye recruitment when compared with competition or 535 536 consumption of Walleye by Rainbow Smelt, and the presence of large Walleye is an indicator of poor recruitment rather than the cause. Little is known about larval Walleye density or 537 competition for prey in Horsetooth Reservoir, though larval Walleye densities were low (~0.5-538 3.5 larvae 1000 m⁻³) during ichthyoplankton sampling near the inlet in 2022 (Lepak et al. 2023). 539

Interestingly, RF model results predicted exceptionally poor Walleye recruitment when peak *Daphnia* densities were below 10 individuals L⁻¹, and zooplankton was dominated by *D. galeata mendotae* rather than *D. pulex* and *pulicaria*. Walleye recruitment indices were below 0.25 fish
net⁻¹ in these cases, which was similar to observations during periods of what was considered
Walleye recruitment "failure" historically.

Intraspecific interactions between Rainbow Smelt include competition for prey resources, and 545 cannibalism of small Rainbow Smelt by larger individuals. Rainbow Smelt cannibalism has been 546 observed widely (e.g. Evans and Loftus 1987; Jones et al. 1994), and may contribute to self-547 548 regulation of population density (Hendersen and Nepszy 1989; He and LaBar 1994). It was evident based on diet data that, especially at smaller sizes, Rainbow Smelt were effective 549 planktivores in Horsetooth Reservoir, and likely compete strongly with other planktivorous 550 551 species and life stages of fish. A distinct enrichment was noted in Rainbow Smelt stable nitrogen isotope values at 130 mm TL, indicating a shift to cannibalism within Horsetooth Reservoir. 552 Thus, large Rainbow Smelt affect recruitment within their own population by functioning as 553 predators and competitors of smaller Rainbow Smelt 554

Mysis diluviana also responded strongly to Rainbow Smelt introduction in Horsetooth 555 556 Reservoir. Rainbow Smelt consume Daphnia and can compete for zooplankton resources with *M. diluviana*, but based on diet information, Rainbow Smelt also consume *M. diluviana* directly. 557 However, M. diluviana can be highly herbivorous or take advantage of detrital resources when 558 559 zooplankton prey are scarce (Hansen et al. 2023). Thus, M. diluviana are likely affected more through Rainbow Smelt predation than resource competition. These factors, in addition to the 560 intermittent presence of a low dissolved oxygen layer near the thermocline; Silver et al. 2021) 561 562 appear to drive the *M. diluviana* population within Horsetooth Reservoir below detection levels

when Rainbow Smelt abundance is high. We are unaware of other reports of such a strong
response by *M. diluviana* in connection with a fish species (e.g. Pothoven et al. 2009; Bruel et al.
2021).

Macrozooplankton populations in Horsetooth Reservoir were restructured by Rainbow Smelt. 566 In particular, the peak density of *Daphnia* in surface waters dropped below 10 individuals L^{-1} , 567 and was accompanied by a complete shift in Daphnia species from D. pulex and pulicaria to 568 generally smaller-bodied D. galeata mendotae. Similar changes in zooplankton communities 569 and their densities in response to Rainbow Smelt have been reported by other investigators (e.g., 570 571 Reif and Tappa 1966; Galbraith 1967). It also appears *Daphnia* density peaks are restricted to periods of peak thermal stratification in mid-to-late summer, which offers *Daphnia* some thermal 572 refuge from Rainbow Smelt and M. diluviana (Johnson and Goettl 1999). However, these 573 periods occur after the time larval Walleye need to transition to consuming larger, preferred 574 Daphnia prey (Johnson and Goettl 1999). Thus, in Horsetooth Reservoir, macrozooplankton 575 restructuring may be creating conditions where organisms like larval Walleye do not have access 576 to prey resources (May et al. 2021). 577

Water storage was a poor predictor of Walleye recruitment. While it is possible that low water 578 579 levels could have disadvantaged Rainbow Smelt disproportionately to Walleye, this was not examined during the reservoir drawdown. Rainbow Smelt did decline prior to the reservoir 580 drawdown, and it is possible declines were perpetuated by low water. It is also possible that the 581 582 longer generation time in Walleye (Scott and Crossman 1973), or a lower reliance Rainbow Smelt on inlet spawning habitat could have allowed Walleye to persist during low water periods 583 and subsequently reproduce and recruit successfully. Walleye recruitment indices in 2001 and 584 585 2004 were the highest observed in over a decade during and following the reservoir drawdown.

586 Walleye and Rainbow Smelt recruitment in relation to future similar drawdowns should be587 studied to help to determine whether similar effects occur.

588 Unintended consequences occurred as a result of Rainbow Smelt stocking in Horsetooth 589 Reservoir. In particular, periods of elevated Rainbow Smelt abundance led to poor Walleye 590 recruitment, and the need to adapt management strategies. Using food web indicators assessed 591 during routine monitoring, managers can preemptively prepare and allocate resources in response 592 to fluctuations in Rainbow Smelt populations.

The predictive framework we developed using an RF model relied on a variety of indices of 593 594 different quality and precision. The model identified the best three predictors of Walleve recruitment as the estimated number of Rainbow Smelt in Horsetooth Reservoir during 595 hydroacoustic surveys (SONAR), the CPUE of large Walleye (LWAL), and the peak density of 596 Daphnia (DAPHd) that preceded the full negative effects from multiple years of poor Walleye 597 recruitment. We acknowledge conditions in Horsetooth Reservoir are unique, but managing in 598 the presence of introduced species is common around the world (Ricciardi and Simberloff 2009). 599 Though predictions can be refined with more or higher quality data, this type of approach could 600 provide managers of other species and systems with the ability to anticipate and prepare for 601 ecological change, particularly if responses to introduced species seem to follow predictable 602 patterns or cycles. 603

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608 **REFERENCES**

Bruel, R., E. Marsden, B. Pientka, N. Staats, T. Mihuc, and J. D. Stockwell. 2021. Rainbow

- Smelt (*Osmerus mordax*) population responses to species invasions and change in environmental
 condition. Journal of Great Lakes Research 47:1171-1181.
- 612
- 613 Cutler, D., R., J. P. Jr. Edwards, K. J. Beard, A Cutler, K. T. Hess, J. Gibson, and J. J. Lawler.
- 614 2007. Random forests for classification in ecology. Ecology, 88(11):2783-2792.
- 615
- DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton:quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic
- 618 Sciences 49:1216-1227.
- 619
- Dick, J. T. A., M. E. Alexander, J. M. Jeschke, A. Ricciardi, H. J. MacIsaac, T. B. Robinson, S.
- 621 Kumschick, O. L. F. Weyl, A. M. Dunn, M. J. Hatcher, R. A. Paterson, K. D. Farnsworth, and D.
- M. Richardson. 2014. Advancing impact prediction and hypothesis testing in invasion ecology
- using a comparative functional response approach. Biological Invasions 16:735-753.
- 624
- Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by
- 626 Rainbow Smelt (*Osmerus mordax*): their freshwater niche and effects on indigenous fishes.
- 627 Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2):249-266.
- 628
- Evans, D. O., and P. Waring. 1987. Changes in multispecies, winter angling fishery of Lake
- 630 Simcoe, Ontario, 1961-83: invasion by Rainbow Smelt, Osmerus mordax, and the roles of intra-
- and interspecific interactions. Canadian Journal of Fisheries and Aquatic Sciences
- 632 44(Supplement 2):182-197.
- 633
- Farrell, C. J., B. M. Johnson, A. G. Hansen, and C. A. Myrick. 2021. Induced triploidy reduces
 mercury bioaccumulation in a piscivorous fish. Canadian Journal of Fisheries and Aquatic
 Sciences 79:200-212.
- 637
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, NewYork. New York Fish and Game Journal 27:105-141.
- 640
- Fournier, A., C. Penone, M. G. Pennino, F. Courchamp. 2019. Predicting future invaders and
 future invasions. Proceedings of the National Academy of Sciences 116(16):7905-7910.
- 643
- 644 Galbraith, M. G. 1967. Selective predation on *Daphnia* by Rainbow Trout and Yellow Perch.
- Transactions of the American Fisheries Society 96:1-10.
- 646
- 647 Gini, C. 1912. Variabilità e mutabilità. Bologna: Tipografia di Paolo Cuppini.
- 648
- 649 Greenwell, B. M. 2017. pdp: An R Package for Constructing Partial Dependence Plots. The R
- 650 Journal 9(1): 421-436.
- 651

- 652 Goettl, J. P., Jr. 1990. Fish forage studies. Colorado Division of Wildlife, Federal Aid in Sport
- Fish Restoration, Project F-53, Job Progress Report, Fort Collins.
- 654
- Goettl, J. P., Jr. 1991. Fish forage studies. Colorado Division of Wildlife, Federal Aid in Sport
 Fish Restoration, Project F-53, Job Progress Report, Fort Collins.
- 657
- Goettl, J. P., Jr. 1992. Fish forage evaluations. Colorado Division of Wildlife, Federal Aid in
 Sport Fish Restoration, Project F-53, Job Progress Report, Fort Collins.
- 660
- Goettl, J. P., Jr. 1993. Fish forage evaluations. Colorado Division of Wildlife, Federal Aid in
 Sport Fish Restoration, Project F-53, Job Progress Report, Fort Collins.
- 663
- Goettl, J. P., Jr., and B. M. Johnson. 1995. Fish forage studies. Colorado Division of Wildlife,
 Federal Aid in Sport Fish Restoration, Project F-240-R2, Job Progress Report, Fort Collins.
- Goettl, J. P., Jr., and B. M. Johnson. 1996. Fish forage studies. Colorado Division of Wildlife,
 Federal Aid in Sport Fish Restoration, Project F-240-R3, Job Progress Report, Fort Collins.
- Goettl, J. P., Jr., and M. S. Jones. 1984. Fish forage evaluations. Colorado Parks and Wildlife
 Federal Aid in Sport Fish Restoration, Project F-53-R, Annual Report, Fort Collins.
- 672
- Goettl, J. P., Jr., and M. S. Jones. 1986. Fish forage studies. Colorado Parks and Wildlife Federal
 Aid in Sport Fish Restoration, Project F-53-R, Annual Report, Fort Collins.
- 675
 676 Goettl, J. P., Jr., and J. Thomas. 1987. Fish forage studies. Colorado Parks and Wildlife Federal
 677 Aid in Sport Fish Restoration, Project F-53-R, Annual Report, Fort Collins.
- 678
- Hansen, A. G., A. McCoy, G. P. Thiede, and D. A. Beauchamp. 2023. Pelagic food web
- 680 interactions in a large invaded ecosystem: implications for reintroducing a native top predator.
 681 Ecology of Freshwater. 32(3):552-570.
- 682
- Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors
- affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–1996. North American
- Journal of Fisheries Management 18:764-774.
- 686
- He, X., and G. W. LaBar. 1994. Interactive effects of cannibalism, recruitment, and predation on
 Rainbow Smelt in Lake Champlain: a modeling synthesis. Journal of Great Lakes Research
 20:289-298.
- 690
- Henderson, B. A., and S. J. Nepszy. 1989. Factors affecting recruitment and mortality rates of
 Rainbow Smelt (*Osmerus mordax*) in Lake Erie, 1963-85. Journal of Great Lakes Research
- 693
 15:357-366.

Hrabik, T. R., J. J. Magnuson, and A. S. McLain. 1998. Predicting the effects of Rainbow Smelt 695 696 on native fishes in small lakes: evidence from long-term research in two lakes. Canadian Journal of Fisheries and Aquatic Sciences 55:1364-1371. 697 698 Johnson, B. M., and J. P. Goettl, Jr. 1999. Food web changes over fourteen years following 699 introduction of Rainbow Smelt into a Colorado reservoir. North American Journal of Fisheries 700 701 Management 19:629-642. 702 Johnson, B. M., J. M. Lepak, and B. A. Wolff. 2015. Effects of prey assemblage on mercury 703 704 bioaccumulation in a piscivorous sport fish. Science of the Total Environment 506:330-337. 705 Jones, M. S. 1985a. Age, growth, and food of Walleye, Smallmouth Bass, and smelt in 706 Horsetooth Reservoir, Colorado. Master's thesis. Colorado State University, Fort Collins. 707 708 Jones, M. S. 1985b. Fish forage evaluations. Colorado Parks and Wildlife Federal Aid in Sport 709 710 Fish Restoration, Project F-53-R, Annual Report, Fort Collins. 711 Jones, M. S., J. P. Goettl, Jr., and S. A. Flickinger. 1994. Changes in Walleye food habits and 712 growth following a Rainbow Smelt introduction. North American Journal of Fisheries 713 Management 14:409-414. 714 715 716 Kirn, R. A., and G. W. LaBar. 1991. Stepped-oblique mid-water trawling as an assessment 717 technique for Rainbow Smelt. North American Journal of Fisheries Management 11:167-176. 718 Lawson, Z. J., and S. R. Carpenter. 2014. A morphometric approach for stocking Walleve 719 fingerlings in lakes invaded by Rainbow Smelt. North American Journal of Fisheries 720 721 Management 34:998-1002. 722 Lepak, J. M., M. B. Hooten, and B. M. Johnson. 2012. The influence of external subsidies on 723 diet, growth and Hg concentrations of freshwater sport fish: implications for fisheries 724 management and the development of fish consumption advisories. Ecotoxicology. 21(7):1878-725 726 1888. 727 Lepak, J. M., A. G. Hansen, E. Cristan, D. Williams, and W. M. Pate. 2023. Rainbow smelt 728 (Osmerus mordax) influence on walleye (Sander vitreus) recruitment decline: mtDNA evidence 729 supporting the predation hypothesis. Journal of Fish Biology. 103:1543-1548. 730 731 Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. R News. 732 733 2(3):18-22. 734 Loftus, D. H., and P. F. Hulsman. 1986. Predation by Rainbow Smelt (Osmerus mordax) on 735 larval Lake Whitefish (Coregonus clupeaformis) and Lake Herring (C. artedii). Canadian 736 Journal of Fisheries and Aquatic Sciences 43:812-818. 737 738

May, C. J., R. R. Budnik, S. A. Ludsin, D. R. O'Donnell, J. M. Hööd, E. F. Roseman, and E. A. 739 740 Marschall. 2021. Evidence that copepod biomass during the larval period regulates recruitment of Lake Erie Walleye. Journal of Great Lakes Research 47:1737-1745. 741 742 Mercado-Silva, N., J. D. Olden, J. T. Maxted, T. R. Hrabik, and M. J. Vander Zanden. 2006. 743 Forecasting the spread of invasive Rainbow Smelt in the Laurentian Great Lakes Region of 744 745 North America. Conservation Biology 20:-1740-1749. 746 747 Mercado-Silva, N., G. G. Sass, B. M. Roth, S. Gilbert, and M. J. Vander Zanden. 2007. Impact 748 of Rainbow Smelt (Osmerus mordax) invasion on Walleye (Sander vitreus) recruitment in Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 64:1543-1550. 749 750 Nalepa, T. F., and D. W. Schloesser, Editors. 2013. Quagga and Zebra Mussels: Biology, 751 Impacts, and Control. CRC Press. Second Edition. 815 p. 752 753 754 Nelson, W. C. 1971. Comparative limnology of Colorado-Big Thompson project reservoirs and lakes. Colorado Department of Game, Fish, and Parks. Fort Collins, Colorado. 755 756 757 Nesler, T. P. 1986. Mysis-gamefish studies. Colorado Parks and Wildlife Federal Aid in Sport Fish Restoration Study F-85-R. Annual Report, Fort Collins. 758 759 760 Parnell, A. 2021. A stable isotope mixing model. Available online: https://cran.rproject.org/web/packages/simmr/index.html, accessed 31 January 2024. 761 762 Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods and 763 764 assumptions. Ecology 83:703-718. 765 Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montana. 766 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in 767 stable isotope analyses. Oecologia 152:179-189. 768 769 770 Pothoven, S. A., H. A. Vanderploeg, S. A. Ludsin, T. A. Höök, and S. A. Brandt. 2009. Feeding ecology of Emerald Shiners and Rainbow Smelt in central Lake Erie. Journal of Great Lakes 771 Research 35:190-198. 772 773 R Development Core Team. 2011. R: A language and environment for statistical computing. R 774 Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, 775 URL:http://www.R-project.org/. 776 777 Reif, C. B., and D. W. Tappa. 1966. Selective predation: smelt and cladocerans in Harvey Lake. 778 Limnology and Oceanography 11:437-438. 779 780 Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an 781 empirical approach applied to zebra mussel invasions. Freshwater Biology 48(6):972-981. 782 783

- Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conversation
- strategy. Trends in Ecology and Evolution 24:248-253.
- 786
- Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada
 11(5):559-623.
- 789
- 790 Rudstam, L. G., S. L. Parker, D. W. Einhouse, L. D. Witzel, D. M. Warner, J. L. Stritzel
- 791 Thomson, D. L. Parrish, and P. J. Sullivan. 2003. Application of in situ target-strength
- estimations in lakes: examples from Rainbow Smelt surveys in Lakes Erie and Champlain. ICESJournal of Marine Science 60:500-507.
- 794

Schneider, J. C., and J. H. Leach. 1977. Walleye, *Stizostedion vitreum vitreum*, fluctuations in
the Great Lakes and possible causes, 1800-1975. Journal of the Fisheries Research Board of
Canada 34:1878-1889.

- 798
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the FisheriesResearch Board of Canada 184:pp 310-317.
- 801

Silver, D. B., B. M. Johnson, W. M. Pate, A. G. Hansen, and K. R. Christian. 2021. History and
outcomes of Opossum shrimp (*Mysis diluviana*) introductions in Colorado. Colorado Parks and
Wildlife Technical Publication No. 58. CPW-R-T-58-21 ISSN 0084-8883. 348 pp.

805

Stacy, W. L., and J. M. Lepak. 2012. Relative influence of prey mercury concentration, prey
energy density and predator sex on sport fish mercury concentrations. Science of the Total
Environment. 437:104-109.

809

810 Stein R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore:

811 exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and

812 Aquatic Sciences. 52(11):2518-2526.

813

Thomas, J. A. 1989. Prey selection by smelt, young Walleye, and young Smallmouth Bass in

815 Horsetooth Reservoir, Colorado. Master's thesis. Colorado State University, Fort Collins.

816 FIGURE CAPTIONS

FIGURE—1. Horsetooth Reservoir bathymetric map. Contours in 10 m intervals. Gill net
locations are numbered circles.

819 FIGURE—2. Horsetooth Reservoir Walleye Sander vitreus diets based on stomach content

analysis (1983–1996) or carbon and nitrogen stable isotope values of Walleye and their prey

analyzed with Bayesian mixing models (2008–2019). Prey item categories (in grayscale) are

822 provided above the figure. Gray boxes indicate periods of relatively high rainbow smelt

abundance. Presence and inclusion of prey items varied by time-period (see Methods for

824 included in "Other invertebrates", and "Other fish").

FIGURE—3. Horsetooth Reservoir predator and prey mean carbon and nitrogen stable isotope

values and standard deviations. The data points and year obtained correspond to colors of the

species information provided in legend. Large (> 130 mm TL) Rainbow Smelt Osmerus mordax

828 data are portrayed with larger sized data points.

FIGURE—4. Horsetooth Reservoir Rainbow Smelt *Osmerus mordax* diets based on stomach

content analysis (1984–1995) or carbon and nitrogen stable isotope values of Rainbow Smelt and

their prey analyzed with Bayesian mixing models (2017–2019). Gray boxes indicate periods of

relatively high Rainbow Smelt abundance. Prey item categories (in grayscale) provided above

the figure were grouped as *Mysis diluviana*, Rainbow Smelt, zooplankton (e.g. daphnids,

copepods), and other invertebrate prey (e.g. dipterans, amphipods).

835 FIGURE—5. Trends in Horsetooth Reservoir Walleye Sander vitreus, Rainbow Smelt Osmerus

836 *mordax, Mysis diluviana, Daphnia*, and reservoir volume. In all panels, gray boxes indicate

periods of relatively high Rainbow Smelt abundance. A) Catch per unit effort of Walleye (150-

300 mm TL) captured during routine gillnetting surveys and standard errors; B) Catch per unit

839	effort of Walleye (\geq 451 mm TL) captured during routine gillnetting surveys and standard errors;
840	C) Walleye length at age-3 from scale interpretation (1980–1991) and otoliths (2001–present)
841	with sample sizes (earlier to later) of 39, 64, 140, 114, 79, 49, 68, 55, 62, 53, 172, 233, 33, 24, 4,
842	3, 2, 7, 22, 22, 18, 19, 50, 35, 32, 46, 41, 20, and 2, respectively. Each cohort mean length at age-
843	3 was plotted three years later to indicate size at age-3 (i.e. data from 1980 represent fish
844	spawned in 1977). Standard error was calculated for data from 2001 to 2016, but only cohort
845	means were available for earlier data; D) Estimates of Rainbow Smelt abundance
846	(hydroacoustics) and density (trawl). Hydroacoustic data (black circles) correspond to the y-axis
847	on the left, and trawl data (white squares) correspond to the y-axis on the right. Standard
848	deviations of trawl surveys are provided; E) Rainbow Smelt encountered during routine
849	gillnetting and boat electrofishing surveys. Indices are represented by the summation of Rainbow
850	Smelt encountered per survey, divided by the number of total surveys that occurred in a given
851	year; F) Estimates of <i>M. diliuviana</i> density (m ⁻²). Standard deviations are provided, and we note
852	that Mysis were collected in 1981 using a benthic trawl (Nesler 1986), and from Rainbow Smelt
853	diets until 1988 (Jones 1985a; Thomas 1989); G) Peak macrozooplankton abundance and
854	dominant Daphnia species measured in Horsetooth Reservoir. Samples dominated by D.
855	pulex/pulicaria are denoted with black circles, and samples dominated by D. galeate mendotae
856	are denoted with white squares; H) Horsetooth Reservoir mean March volume (km ³). Photo
857	credits: B. Swigle, Colorado Parks and Wildlife (A, and B); A. Hansen, Colorado Parks and
858	Wildlife (C, D, and E); Per Harald Olsen, no modifications,
859	https://creativecommons.org/licenses/by-sa/3.0/ (F); Anita Pearson, New Zealand Department of

860 Conservation (G); M. Koski and B. Johnson, Colorado State University (H).

861	FIGURE—6. Variable importance metrics for Walleye Sander vitreus recruitment predictors.
862	Metrics included percent increase in mean square error (%) and increase in node purity.
863	Predictors evaluated included gill net catch rates of large (\geq 451 mm TL) Walleye (LWAL),
864	estimated number of Rainbow Smelt Osmerus mordax based on hydroacoustic surveys
865	(SONAR), Rainbow Smelt encountered during routine sampling efforts (RSM), estimated Mysis
866	diluviana density (MYSIS), the maximum Daphnia density observed (DAPHd), the percent of
867	D. pulex/pulicaria from that maximum (DAPHc), and reservoir water capacity (H2O). See
868	Figure 5 caption for photo credits.
869	FIGURE—7. Random forest (RF) predictions of Walleye Sander vitreus recruitment (number of
870	Walleye 150–300 mm TL caught per net set during surveys) in Horsetooth Reservoir as a
871	function of estimated recruitment. Predicted recruitment was generally lower (to the right of the
872	dashed 1:1 line) at higher estimated recruitment, and higher (to the left of the 1:1 line) at lower
873	estimated recruitment. See Figure 5 caption for photo credits.
874	FIGURE—8. Partial dependence plots for the best three predictors of Walleye Sander vitreus
875	recruitment (number of Walleye 150-300 mm TL caught per net set during surveys) in
876	Horsetooth Reservoir. Partial dependence of predictions are plotted as a function of the estimated
877	recruitment based on hydroacoustic surveys (SONAR; A), number of large Walleye captured
878	during spring gillneting surveys (LWAL; B), and peak density of Daphnia during
879	macrozooplankton surveys (DAPHd; C). See Figure 5 caption for photo credits.

880 Figure 1.







Figure 3.










Figure 7.







Figure S1. Horsetooth Reservoir storage. The black line indicates daily water storage (km³) in
Horsetooth Reservoir through time. Drawdown conditions are notable from 2001-2003. The plot
begins 1 January 1980.

901 Linear Interpolation

Linear interpolation was used to fill in missing data (n=40) for the RF analysis. However,

when a value came either first or last in a data series, and there were missing values outside that

range (n=10), linear extrapolation was used to fill in the data series from 1982–2023. Exceptions

- to these conditions included the metric for Walleye recruits. Walleye fingerlings were stocked in
- 1994–1997, and likely artificially elevated the catch rates of 150–300 mm TL Walleye in the
- 907 mid- to late 1990s. Thus, this metric was set to 0.05 (reflective of natural reproduction measured
- in 1994 from 1993), for missing values in 1995 and 1996. Measured values of 0.45 both in 1994

909	and 1997 were set to the measurement of natural reproduction (0.05) measured from the 1993
910	cohort in 1994 netting. Hydroacoustic data were first collected in 1994, but up until 1983, the
911	Rainbow Smelt population was zero, and this value was used for linear interpolation in this case.
912	The benthic trawl data collected in 1981 were used by Nesler (1986) to calculate a conservative
913	density of Mysis diluviana of 1.75 m ⁻² . This value was applied from the beginning of the data set
914	until 1988, when M. diluviana were no longer observed in Rainbow Smelt diets. The value zero
915	was used from 1988–1999 when zero M. diluviana were observed during more rigorous, routine
916	sampling. This time period was one of high Rainbow Smelt density, and the assumption of M .
917	diluviana density being low is likely valid. Finally, water capacity for Horsetooth Reservoir was
918	available from 1983 to 2023, and 1983 data were used to reflect 1982 conditions.
919	In addition to the exceptions noted above, linear interpolation was used to fill gaps in the data
920	set. For Walleye recruitment there were four instances of this, for LWAL there were seven
921	instances, for SONAR there were 11 instances, for RSM there were four instances, for MYSIS
922	there were nine instances, for both DAPHd and DAPHc there were five instances in addition to
923	the 10 instances requiring extrapolation (five instances for each from 1982–1986). The linear
924	interpolation approach was selected primarily because of the observed and relatively complete
925	regime shifts when Rainbow Smelt abundance was high.

RESEARCH PRIORITY:Food webs and predator-prey interactions (Part 2):
Rainbow Smelt Osmerus mordax – Walleye interactions 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.

MANUSCRIPT PREPARED FOR SUBMISSION

Walsworth, T. E., A. G. Hansen, and J. M. Lepak. Life-stage dependent impacts of prey species drive cyclic dynamics of a top predator population. Submitting to Canadian Journal of Fisheries and Aquatic Sciences.

FULL MANUSCRIPT

- 1 Title
- 2 Life-stage dependent impacts of prey species drive cyclic dynamics of a top predator population
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- 8 Competing Interests
- 9 The authors declare there are no competing interests.

10 Author Contributions

- 11 Conceptualization TW, AH, JL; Data curation AH, JL; Formal analysis TW; Methodology TW, AH, JL;
- 12 Visualization TW, AH, JL; Writing original draft TW, AH, JL; Writing review and editing TW, AH, JL
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- 15 Data Availability Statement
- 16 Data generated or analyzed during this study are available from the corresponding author upon
- 17 reasonable request.

18 Abstract

- 19 The establishment of species acting as competitors, predators, and prey to different life-stages of top
- 20 predator species can produce alternative ecosystem states, presenting significant challenges to fisheries
- 21 management. The establishment of rainbow smelt Osmerus mordax in Horsetooth Reservoir (Colorado,
- 22 USA) has resulted in cyclic abundance and recruitment dynamics of a prized top predator, walleye
- 23 Sander vitreus. Here, we apply a time-varying, stage-structured population model to 42 years of data to
- 24 characterize the relationships between dynamic ecosystem conditions and walleye vital rates,
- abundance, and size-structure, ultimately identifying two distinct ecosystem states. One state, occurring
- 26 when smelt densities are low and Daphnia densities are high, supports strong walleye recruitment, but
- 27 little growth and survival to larger size-classes. The second state, occurring under high smelt densities
- and low Daphnia densities, supports limited recruitment, but increased growth and survival to larger
- 29 size-classes. While larger size-classes of walleye benefit from the presence of abundant smelt prey,
- 30 smaller size-classes suffer from increased predation and competition. These results can inform future
- 31 harvest regulations and walleye stocking strategies to maintain consistent fishery quality.

32 Introduction

33 The behavioral and physiological effects of increasing body size throughout the lifetime of individuals 34 (e.g., changes in diet, habitat selection, mortality, fecundity) can drive complex population and 35 community dynamics (e.g., De Roos et al. 2008; Guill 2009; Abrams 2011). Individuals of many species 36 undergo ontogenetic diet shifts (Sánchez-Hernández et al. 2019), as increasing body size reduces their 37 susceptibility to predation and reduces morphological constraints on consuming larger, more energy 38 dense prey (Werner and Gilliam 1984; Galarowicz et al. 2006; Gaeta et al. 2018). The availability of 39 larger prey can have major impacts on the growth and survival of species undergoing ontogenetic diet shifts (Post 2003; Huss et al. 2013), with implications for population dynamics. Ontogenetic shifts in 40 41 predator species that have small offspring can produce systems of life history intraguild predation 42 (LHIGP), where juveniles of the predator compete with species that ultimately serve as prey for adults (e.g., Polis and Holt 1992; Abrams 2011). Theoretical models of life history intraguild predation produce 43 44 alternative stable states and cyclic dynamics, in which small changes in predator mortality, cannibalism 45 rates, competitive imbalance, or productivity can shift the system between predator-present and 46 predator-absent states or limit cycles (e.g., Abrams 2011; Toscano et al. 2016, 2017). While much of the 47 support for the complex dynamics resulting from life history intraguild predation comes from theoretical 48 models (Van de Wolfshaar et al. 2006; Abrams 2011; Hin et al. 2011) and simple experimental 49 communities (Toscano et al. 2016; Toscano and Rudolf 2021), it has also been suggested to be 50 responsible for regime shifts among alternative states in natural populations (Walters and Kitchell 2001). 51 The prevalence of life history omnivory among piscivorous fishes (e.g., Galarowicz et al. 2006; Post 2003; 52 Huss et al. 2013) presents the opportunity for LHIGP dynamics to exert strong effects on the recreational 53 or commercial value of fisheries via impacts on recruitment (e.g., Polis and Holt 1992; Walters and 54 Kitchell 2001; Baskett et al. 2006).

55

Predicting recruitment of offspring to the adult population is a critical component of effective fisheries management (Hilborn and Walters 1992; Plagányi et al. 2019), as recruitment dynamics influence sustainable exploitation rates and the resilience of populations to disturbance. Despite its importance to effective management decisions, uncovering the drivers of annual recruitment dynamics remains challenging for multiple reasons, including among-population variability in the critical determinants of recruitment (Hansen et al. 2018; Honsey et al. 2020), and non-stationarity of conditions driving recruitment within populations (e.g., Szuwalski and Hollowed 2016; Zhang et al. 2018). Recent decades 63 have seen declining or highly variable recruitment rates of walleye Sander vitreus across many ecosystems, threatening the sustainability of many culturally and economically valuable recreational and 64 65 subsistence fisheries across their range (Embke et al. 2019; Cahill et al. 2022; Mrnak et al. 2023). Identifying the drivers of recruitment declines and the potential of different lakes to support walleye 66 production under expected future conditions has thus been a focus of research and management 67 68 activities for the past two decades (Hansen et al. 2015; Feiner et al. 2019; Krabbenhoft et al. 2023). 69 Previous work has identified multiple abiotic (e.g., temperature, spring warming rate, winter conditions, 70 water levels) and biotic (e.g., spawning stock, predation, competition, invasive species) as drivers of 71 walleye recruitment dynamics in at least some ecosystems (reviewed in Krabbenhoft et al. 2023). 72 Rainbow smelt Osmerus mordax, a species widely introduced to support the forage base of piscivorous 73 sport fish, have repeatedly been demonstrated to negatively impact walleye populations through 74 competition and predation on young life stages (Schneider and Leach 1977; Colby et al. 1987; Johnson 75 and Goettl 1999; Mercado-Silva et al. 2007; Lepak et al. 2023). As rainbow smelt can take the roles of 76 predator, competitor, and prey for different size classes of walleye (Johnson and Goettl 1999; Mrnak et 77 al. 2023; Lepak et al. 2023; Lepak et al. in press), their presence in lakes supporting walleye populations 78 has the potential to drive complex dynamics, including alternate states.

79 Horsetooth Reservoir (near Fort Collins, CO, USA) has supported a popular walleye fishery since the 80 1950s, and rainbow smelt were introduced in 1983 to provide forage for the walleye and smallmouth 81 bass populations of the reservoir. Increasing abundance of rainbow smelt through the late 1980's and 82 early 1990's drove major changes to Horsetooth Reservoir's fish community and food web structure 83 (e.g., Johnson and Goettl 1999; Lepak et al. in press). Rainbow smelt compete with young walleye for 84 zooplankton prey, reducing the abundance of preferred Daphnia spp. (Lepak et al. in press), and prey 85 upon age-0 walleye (Lepak et al. 2023). However, larger walleye prey heavily on rainbow smelt and 86 demonstrate elevated growth rates and greater abundance when rainbow smelt are abundant (Lepak et 87 al., in press). Thus, rainbow smelt have distinct and divergent impacts on different size-classes of 88 walleye, and cyclic dynamics of rainbow smelt abundance have occurred alongside alternating periods of 89 low recruitment, high adult abundance and high recruitment with low adult abundance for walleye in 90 Horsetooth Reservoir (Lepak et al., in press). These two states provide very different fishery values and 91 present fisheries management trade-offs (lack of recruitment with abundant quality sized fish vs. 92 consistent recruitment with rare quality sized fish). Understanding how recruitment, growth and survival

93 of walleye are impacted by cyclic food web dynamics may inform future management efforts aiming to
94 maintain recreational fishery values.

95 Here, we develop a time-varying stage-structured population model characterized by a binary latent 96 ecosystem state to disentangle cyclic dynamics observed across multiple trophic levels. We analyze data 97 from three trophic levels and multiple life-stages in the aquatic community of Horsetooth Reservoir 98 collected across 42 years. Specifically, we examine (1) how changes in abundance at lower trophic levels 99 affect the vital rates of different life stages of the top predator, (2) whether latent changes in ecosystem 100 state can drive cyclic dynamics across life-stages of the top predator, and (3) how observations of lower 101 trophic levels can be used to predict the current state of the ecosystem and therefore how we would 102 expect the top predator population to change. The results of our work are broadly relevant to 103 understanding the population dynamics of size, stage, or age-structured populations experiencing non-104 stationary ecosystem conditions, and can directly inform the management of the fishery in Horsetooth 105 Reservoir.

106

107 Methods

108 Study Site

109 Horsetooth Reservoir is a large (capacity of ~200 million m³) reservoir in north central Colorado, located 110 in the Rocky Mountain Foothills near Fort Collins (Larimer County), CO. The reservoir has three relatively 111 distinct basins and water enters the system through the Hansen Feeder Canal then moves north to the 112 Fort Collins and Tri-Districts Water Treatment Facilities and the Hansen Supply Canal (Fig. 1). The 113 reservoir has a mean depth of 25 m and a maximum depth of 70 m, typically stratifying thermally in 114 early spring through late October or early November. Horsetooth Reservoir functions as a municipal 115 water source and provides water for irrigation/agriculture purposes as well as recreation. Horsetooth 116 Reservoir was traditionally managed as a two-tiered fishery supported by naturally reproducing walleye 117 and stocked salmonids (kokanee salmon Oncorhynchus nerka and rainbow trout O. mykiss). Salmonid 118 stocking was diminished around 2000, and walleye now represent a primary target for harvest versus other species. The Horsetooth Reservoir fish community is also represented by naturally reproducing 119 120 smallmouth bass (*Micropterus dolomieu*), other centrarchids like bluegill sunfish (*Lepomis macrochirus*), 121 yellow perch (Perca flavescens), and importantly, rainbow smelt, introduced in 1983 to improve 122 smallmouth bass and walleye growth, which was successful for walleye (Jones et al. 1994).

123 Data: Walleye Catch

124 Walleye catch data were obtained from gillnetting surveys conducted most years in late April-May in 125 Horsetooth Reservoir (Jones et al. 1994). Generally, a set of 20 standardized monofilament gill nets were 126 used measuring ~46 m long and ~1.8 m high, with 6 graduated panels ranging from 13-76 mm bar-mesh 127 and increasing in 6-13 mm increments. Historically, effort was often recorded as "overnight" for each 128 net rather than the hours and minutes of soak time (Lepak et al. in press). Thus, this metric (number of 129 walleye per gill net set overnight) was used for comparison through time. Three different size classes of 130 walleye; 150-300 mm (indicative of predominantly age-1 walleye recruits; our unpublished data), 301-131 450 mm (larger individuals still shorter than a common minimum length limit for walleye), and \geq 451 132 mm (indicative of adult reproductive walleye with elevated growth rates and vulnerable to harvest 133 under current management) were considered to mimic previous comparisons (i.e., Johnson and Goettl 134 1999), and characterize walleye population dynamics.

135

136 Data: Daphnia density

137 Sampling for large-bodied Daphnia (relevant as forage for rainbow smelt and young walleye) was 138 conducted mid-morning predominantly from April-September (monthly) with a metered Clarke-Bumpus 139 sampler from 1987-1996 (Johnson and Goettl 1999). Zooplankton tend to be concentrated near the 140 surface (< 10 m) in Horsetooth Reservoir (e.g., Nelson 1971; Johson and Goettl 1999). Thus, from 1987-141 1993, the upper 0-5 m were sampled, while in 1994-1996, samples were taken from 0-10 m. 142 Zooplankton sampling from 2002-2018, and 2020, 2022, and 2023 was analogous to 1987-1996 (but 143 using a 153 µm Wisconsin net), and represent a compilation of data collected from Colorado State 144 University personnel (0-10 m sampled), and the Bureau of Reclamation and Northern Colorado Water 145 Conservancy District (data collected from 0-5 and 0-10 m). In 2019 and 2021 analogous surveys (153 μm 146 Wisconsin net from 0-10 m) were conducted by Colorado Parks and Wildlife personnel. Horsetooth 147 Reservoir has three distinct basins (Fig. 1), and zooplankton were sampled from each basin and 148 averaged across basins when feasible. Since the timing of the highest density of Daphnia observed 149 varied (May-September), the sampling occasion from each year with the highest estimated mean 150 density of Daphnia (individuals L⁻¹) was used as the index for zooplankton. Observed Daphnia densities 151 were multiplied by 2 to make the minimum non-zero observation equal to 1, maintaining relative 152 differences among small observations as scaled densities were then rounded to nearest whole number

for use with the negative binomial error structure in our model (*see below*). We note that such scalar adjustments do not impact our interpretation of model results because we are not attempting to estimate true abundances of the different stages of walleye, rainbow smelt, or *Daphnia* and smelt populations, but rather the relationships between them.

157 Data: Rainbow smelt abundance

158 Rainbow smelt abundance has been monitored with multiple protocols across the duration of the study 159 period, and initially, trawl surveys were conducted (1983-1996). These surveys took place at night in late 160 August (with the exception of 1993, 1995, and 1996 October surveys set to coincide with hydroacoustic 161 data) using a net 6 x 6 m at the opening and graduated mesh from 203 mm (stretch) to 13 mm at the 162 cod end. The trawl was deployed 4-8 times annually in a stepped-oblique fashion (0-6, 6-12, 12-18 m) 163 from the surface to 18 m towing at ~1 m/s for 5 minutes at each depth stratum (Kirn and LaBar 1991; 164 Johnson and Goettl 1999). Rainbow smelt densities were multiplied by reservoir volume to estimate 165 abundance. Hydroacoustic surveys (1993-1996) were conducted in October (with the exception of the 166 1994 August survey) with a BioSonics 420 kHz, dual-beam echosounder and analyzed using echo 167 integration with *in situ* trawl catch data to determine mean rainbow smelt body size and target strength 168 (-50 dB; Johnson and Goettl 1999). These surveys and the trawl surveys were conducted in four of the 169 same years, allowing for comparison and calibration of the two methods in our model. Subsequent 170 hydroacoustic surveys (1998-2013) were conducted similarly, but with a 200 kHz Hydroacoustic 171 Technology Incorporated Model 243 split beam digital echosounder and real-time target tracking 172 algorithm. Fish targets were identified and target strengths corresponding to individuals > 5 cm and < 20 173 cm based on fine mesh gill net catches and a target strength-length relationship for rainbow smelt 174 (Rudstam et al. 2003). From 2017-2023, surveys were conducted with the same equipment, but during 175 peak stratification (July-August) using echo integration (versus target tracking) to enumerate rainbow 176 smelt. Data were also collected following zig-zag transects (versus longitudinal transects down the 177 middle of the reservoir). Rainbow smelt density estimates were extrapolated from these data to 178 estimate abundance. The resultant abundance estimates from all surveys were rounded to the nearest 179 whole number for use with the negative binomial error structure in our model (see below).

180 Population Model

181 Given the binned size-structural nature of the walleye data, we assumed the Horsetooth Reservoir

182 walleye population followed stage-structured population dynamics, in which a proportion of individuals

183 survive transition to the next largest size-class. Additionally, we assumed that the probabilities of

184 survival and transitioning to subsequent stages were dependent on the underlying ecosystem state,

represented by a binary, latent variable. The probability of being in either ecosystem state is predicted

186 by the relative abundances of Daphnia spp. and rainbow smelt.

187

188 Stage-structured population dynamics

We assumed walleye occupied one of four stages, age-0, small (150-300mm), medium (300-450mm), or
 large (> 450 mm). The number of individuals in all stages except age-0 at each time step is described by:

$$N_{a\neq 1,t} = N_{a-1,t-1}s_{a-1,t-1}g_{a-1,t-1} + N_{a,t-1}s_{a,t-1}(1 - g_{a-1,t-1})$$
(1)

where $N_{a,t}$ is the number of individuals in stage *a* during time *t*, *s* is the survival rate, and *g* is the probability of transitioning to the next stage. We assumed the probability of large walleye transitioning to the next stage (g_{4,t}) to always equal zero, as all individuals greater than 450 mm were included in this stage. Both survival rates and probabilities of transitioning among stages varied by stage and by ecosystem state.

196 The number of individuals in the age-0 stage $(N_{1,t})$ was characterized by a Beverton-Holt spawner-197 recruitment relationship in which both medium $(N_{3,t})$ and large $(N_{4,t})$ walleye stages contribute to 198 spawner abundance:

$$N_{1,t} = \frac{\alpha(N_{3,t} + N_{4,t})}{1 + \varphi(N_{3,t} + N_{4,t})}$$
(2)

199 where α and φ are estimated parameters.

As there were no independent estimates of total abundance available to anchor our model estimates, we fixed the survival rate of age-0 individuals in ecosystem state 1 ($s_{a=1,\gamma=1}$) to equal 1. As such, age-0 survival rate estimates from our model should not be interpreted as true survival estimates, but rather as relative survival rates across ecosystem states. The survival rate of age-0 individuals in ecosystem state 2 ($s_{a=1,\gamma=2}$) was freely estimated from a uniform beta distribution:

$$s_{1,2} \sim Beta(1,1)$$
 (3)

To reduce model parameterization, we assumed survival rates of larger stages in both ecosystem states
 followed logistic relationships:

$$s_{a\neq 1,\gamma} = \frac{exp(\beta_{0,\gamma} + \beta_{1,\gamma}a)}{1 + exp(\beta_{0,\gamma} + \beta_{1\gamma}a)}$$
(4)

where $\beta_{0,\gamma}$ and $\beta_{1,\gamma}$ are estimated parameters describing the relationship between stage and survival of individuals in stage *a* in ecosystem state γ .

209 We assumed all individuals in the age-0 stage transitioned to the small stage ($g_{a=1} = 1$) and that all

individuals in the largest stage remained in that stage ($g_{a=4} = 0$). For the small and medium stages, we

assumed that the probabilities of transitioning to the next largest stage in both ecosystem states

212 followed logistic relationships:

$$g_{a,\gamma} = \frac{exp(\omega_{0,\gamma} + \omega_{1,z}a)}{1 + exp(\omega_{0,z} + \omega_{1,z}a)}$$
(5)

213 where $\omega_{0,\gamma}$ and $\omega_{1,z}$ are estimated parameters describing the relationship between stage and

214 probability of transitioning to subsequent stages *a* in ecosystem state γ .

215 We assumed that the number of individuals captured during surveys was linearly related to abundance,

216 effort, and vulnerability of each stage to capture:

$$C_{a,t} = N_{a,t} v_a E_t \tag{6}$$

217 where $C_{a,t}$ is the number of stage *a* individuals captured at time *t*, v_a is the vulnerability of stage *a* individuals to capture, and E_t is the level of sampling effort expended in time t. We assumed that 218 219 vulnerability of individuals in the age-0 stage was zero, as they are not reported in the catch, and that 220 vulnerability of large individuals (v₄) was equal to 1 divided by the maximum sampling effort across 221 years (such that $v_4 E_t = 1$ in years with maximum survey effort) to anchor our abundance estimates 222 when no independent estimates of abundance were available. As such, vulnerability estimates should be 223 considered relative, not absolute, estimates. Vulnerability of the small and medium stages were freely 224 estimated from a uniform beta distribution:

$$v_2 \sim Beta(1,1),$$
 (7)

$v_3 \sim Beta(1,1)$.

225

- 226 Latent Ecosystem State
- 227 We assume that the binary latent ecosystem state impacting stage-specific survival and transition
- 228 probabilities can be predicted from Daphnia and smelt densities:

$$logit(p_{\gamma_t=1}) = \beta_{0,state} + \beta_{Daphnia} D_{t,rel} + \beta_{smelt} \psi_{t,rel}$$

$$D_{t,rel} = \frac{D_t}{D_{max}} \tag{8}$$

$$\psi_{t,rel} = \frac{\psi_t}{\psi_{max}}$$

- where $p_{\gamma_t=1}$ is the probability that the ecosystem is in state 1 at time t, $\beta_{0,state}$ is an estimated intercept parameter, $\beta_{Daphnia}$ and β_{smelt} are the logistic regression slopes for the effect of Daphnia and rainbow smelt densities, respectively, D_t is the density of Daphnia at time t, $D_{t,rel}$ is the density of Daphnia at time t relative to the maximum density of Daphnia across the time series (D_{max}), ψ_t is the abundance of rainbow smelt at time t, and $\psi_{t,rel}$ is the abundance of rainbow smelt at time t relative to the maximum abundance of rainbow smelt across the time series (ψ_{max}).
- As we do not have estimates of either Daphnia density or rainbow smelt abundance for all years within
 our data set, we estimated annual densities for both taxa with random walks:

$$log(D_t) \sim N(log(D_{t-1}), \sigma_D^2),$$

$$log(\psi_t) \sim N(log(\psi_{t-1}), \sigma_S^2),$$
(9)

237 where σ_D^2 and σ_S^2 are estimated parameters describing the variance of the random walk for each taxa.

238

239 Likelihoods

240 We assumed that observed catch of walleye at each stage, Daphnia densities, and rainbow smelt

241 densities were negative binomially distributed around the model predicted values:

$$L(\hat{C}_{a,t}|\theta) \sim NB(P_{c,a,t}, r_c),$$

$$P_{c,a,t} = \frac{r_c}{(r_c + C_{a,t})}$$
(10)

$$L(\widehat{D}_t | \theta) \sim NB(P_{D,t}, r_d),$$

$$P_{d,t} = \frac{r_d}{(r_d + D_t)}$$
(11)

243

$$L(\hat{\psi}_{t,sonar}|\theta) \sim NB(P_{s,t}, r_s),$$

$$P_{s,t} = \frac{r_s}{(r_s + \psi_t)}$$
(12)

244

$$L(\hat{\psi}_{t,trawl}|\theta) \sim NB(P_{s,t}, r_s),$$

$$P_{s,t} = \frac{r_s}{(r_s + q_{trawl}\psi_t)}$$
(13)

where $\hat{C}_{a,t}$ is the observed catch of walleye in stage *a* at time *t*, \hat{D}_t is the observed Daphnia density at time *t*, $\hat{\psi}_{t,sonar}$ is the observed smelt density from SONAR surveys at time *t*, $\hat{\psi}_{t,trawl}$ is the observed smelt density from trawl surveys at time *t*, q_{trawl} is an estimated parameter scaling observed trawl densities to the magnitude of observed SONAR densities, θ is a vector of all model parameters, P_x is the negative binomial shape parameter for each data type *x*, and r_x is the negative binomial rate parameter for each data type *x*.

251 We fit the population model in JAGS (Just Another Gibbs Sampler, Plummer 2003), implemented

through the R Programming Environment (R Core Team 2022), using the rjags (Plummer 2023), runjags

253 (Denwood 2016), and R2jags (Su and Yajima 2022) packages.

255 Simulation model: Predicting ecosystem state from observations of lower trophic levels 256 We conducted simulations to characterize the ability of managers to assess the probability of the 257 ecosystem being either of the two latent states based on field observations of Daphnia or rainbow smelt 258 densities. We determined the probability of the ecosystem being in the first state across a range of 259 observed Daphnia and smelt densities. In each iteration of our simulation, we sampled a "true" Daphnia 260 and smelt density as a function of the relative likelihoods of a range of "true" values given the specified 261 observed values and model estimated uncertainty from the negative binomial shape and rate 262 parameters described above. We then calculated the probability that the ecosystem was in state 1 using 263 eqn. [8]. For each iteration, we used one sample from the posterior distribution for our model 264 parameters, and used the maximum Daphnia and smelt densities from that posterior sample to 265 calculate the relative densities of the simulated "true" densities needed for eqn. [8]. We repeated this 266 simulation 1000 times for each combination of observed Daphnia and smelt densities, and conducted 267 the simulation model in the R Programming Environment (R Core Team 2022).

268

- 269 Simulation model: Effect of state duration on long-term walleye abundance trends
- We used the parameter estimates from our population model to examine the impact of different state
 duration lengths on the probability that the population of large walleye would increase. We specified a
- range of periodicities from 0 to 10 years, and simulated the population forward for 100 years under all
- possible combinations of state duration for both states (i.e., state 1 period = 0-10 years, state 2 period =
- 0-10 years). We simulated the population using all MCMC posterior parameter combinations. For each
- simulated time series, we fit a linear regression to the abundance of large walleye across the last 50
- 276 years of the simulation. We then calculated the proportion of regression slopes that were greater than 0
- 277 for each combination of duration lengths for the two states.
- 278

279 Results

- 280 Walleye Vital Rates
- 281 Annual survival rates of different stages of walleye varied among ecosystem states. Ecosystem state 1 is
- characterized by high age-0 survival (specified to equal 1 in our model) and declining survival across
- subsequent larger stages (Fig. 2a; small walleye median survival = 0.952 [95% Cl = 0.484 0.991];
- 284 medium walleye 0.852 [0.447 0.932]; large walleye 0.613 [0.320 0.748]). Conversely, estimated

relative survival of age-0 walleye in ecosystem state 2 was very low (median = 0.012, 95% CI = 0.000 -

286 0.055), while survival increased across larger stages (small walleye 0.560 [0.254 - 0.771]; medium

287 walleye 0.790 [0.700 - 0.887]; large walleye 0.915 [0.830 - 0.988]). Survival of small walleye was higher

in ecosystem state 1 than state 2, was similar between the two states for medium-sized walleye, and

289 was higher in state 2 than state 1 for large walleye. Hereafter, we refer to ecosystem state 1 as the "high

290 recruitment" state and ecosystem state 2 as the "high adult survival" state.

291 The probability of transitioning to the next stage (i.e., size-class) also varied across ecosystem states (Fig.

292 2b). Small and medium-sized walleye were more likely to grow into the next size class in the high adult

survival state (small walleye median transition probability 0.356 [95% CI = 0.124 - 0.794]; medium

walleye 0.132 [0.071 -0.212]) than in the high recruitment state (small walleye 0.006 [0.000 - 0.731];

295 medium walleye 0.008 [0.000 - 0.079]). The probability of small individuals transitioning to medium sizes

296 was greater in both ecosystem states than was the probability of transitioning from medium to large

297 sizes.

Walleye recruitment is predicted to increase with increased spawning abundance (Fig. 2c), though there is large uncertainty in the relationship. The Beverton-Holt relationship is not predicted to saturate within the range of spawning abundances predicted throughout the time-series. However, the number of small walleye recruiting to the population during periods of high spawner abundance is limited by the extremely low survival of age-0 walleye in the high adult survival state (Fig. 2a), effectively producing over-compensatory dynamics.

304

305 Rainbow Smelt and Daphnia abundance time-series

306 The random walk process was able to effectively reproduce the observed rainbow smelt and Daphnia 307 population dynamics while providing estimates of their abundance during unobserved periods (Fig. 3ab). 308 Our model predicts that rainbow smelt abundance started out very low in the early 1980s before rapidly 309 expanding to 58.8 million individuals (95% CI = 9.69 - 248.32 million) at their highest point in 1989, 310 before they declined to low levels again by 1998 (median abundance estimate = 36 975; 95% CI = 12 488 311 - 285 201). Rainbow smelt abundances slowly increased again through 2020, before modestly declining 312 in recent years. The second rainbow smelt abundance peak is not predicted to have been as large as the 313 first peak (Fig. 3a).

Daphnia densities at the beginning of the time series are highly uncertain, as there are no observations

available before 1987. Our model predicts Daphnia abundances to have slowly decreased until the late

316 1980s, when they declined rapidly to low densities which persisted until 1994. The model predicts

317 Daphnia underwent alternating low (1996-2004, 2011-2022) and high (2005-2010) abundance states

since the mid-1990s (Fig. 3b).

319

320 Ecosystem State

321 The two latent ecosystem states are predicted by opposing patterns of Daphnia and rainbow smelt 322 abundances (Fig. 3cd). The probability of being in the high recruitment state increases when Daphnia 323 densities are elevated (Fig. 3c) and when rainbow smelt abundance is reduced (Fig. 3d). The predicted 324 probability of being in the high recruitment state has undergone three large and sustained shifts across 325 the period of record, representing transitions between alternative ecosystem states (Fig. 3e). Our model 326 estimates the ecosystem was in the high recruitment state from 1982 until 1988 and from 1995 until 327 2011, being in the high adult survival state during the intervening periods. The probabilities of being in 328 either ecosystem state are more equivalent and uncertain during transition periods between states. 329 Interestingly, the predicted ecosystem state often transitioned before the predicted probability of being 330 in the high recruitment state based on Daphnia and rainbow smelt abundances changed (Fig. 3e).

331

332 Walleye Abundance and Catch

333 The vulnerability of walleye to survey gears increased with size, as individuals in the medium stage 334 (median catchability estimate = 0.038; 95% CI = 0.019 - 0.043) were much more likely to be captured 335 than were those in the small stage (median catchability estimate = 0.002; 95% CI = 0.0004 - 0.007; Fig. 336 2d). Our model was able to effectively recreate the observed time-series of catch across all three 337 observed stages (Fig. 4), as all but one observed catch value fell within the posterior predictive 338 distributions. Small walleye dynamics (Fig. 4b) were predicted to be more variable across years than 339 were medium and large walleye, being more influenced by annual recruitment anomalies. The model 340 effectively reproduces the alternating periods of high and low catch for both the medium (Fig. 4c) and 341 large (Fig. 4d) walleye stages.

343 Simulation model: Predicting ecosystem state from observations of lower trophic levels 344 Our simulation model predicting the probability of the ecosystem occupying the high recruitment state 345 given observed rainbow smelt and Daphnia densities predicts a gradual shift from high to low 346 probabilities as both Daphnia densities decline and rainbow smelt densities increase (Fig. 5). Observed 347 Daphnia and rainbow smelt densities are moderately negatively correlated (r = -0.48 for when using 348 smelt estimates from sonar surveys, r= -0.274 when using smelt estimates from trawling surveys), such 349 that the ecosystem has generally been observed to be in either a high Daphnia, low smelt state 350 (corresponding to higher probability of being in the high recruitment state), or a low Daphnia, high 351 rainbow smelt state (corresponding with a high probability of being in the high adult survival state; Fig. 352 5). However, several years of observations fall very near the line demarcating when the system is more 353 likely to be in one state or the other, corresponding largely to years when the ecosystem is transitioning

355

354

among states (Fig. 3e).

Simulation model: Effect of state duration on long-term walleye abundance trends 356 357 The relative duration of periods spent in the two different states had a major impact on the expected 358 long-term trend in large walleye abundance (Fig. 6). The probability of long-term increases in walleye 359 abundance was greatest when the duration of each period in state 2 was approximately 50% of the 360 duration of periods spent in state 1. Scenarios with slightly longer durations in state 2 were able to 361 produce positive regression slopes in approximately 50% of simulations, suggesting these combinations 362 produced stable long term dynamics. However, all scenarios in which the period duration of state 2 was 363 five years or greater had less than 50% probability of long-term abundance increase, suggesting periods 364 longer than five years for state 2 lead to long-term declines in the walleye population.

365

366 Discussion

The tendency of ecosystems to express alternative states providing substantially different ecosystem services presents significant obstacles to fisheries management agencies tasked with maintaining fish stocks and fishing opportunities. The Horsetooth Reservoir walleye fishery examined here has been characterized by cycles between two distinct states demonstrating large differences in stage-specific walleye vital rates over the past four decades. These alternative states appear to be maintained by lower trophic level conditions, as transitions among states can be predicted by Daphnia and rainbow

smelt abundances. The relationship between lower trophic levels and ecosystem state suggests a food
web mechanism is maintaining the states, though transitions between states may be triggered by
additional drivers we did not explore. By identifying the presence and predictors of the alternative
ecosystem states, our results can inform short-term management decisions for the walleye fishery, and
provide an approach that can be applied to other ecosystems.

378

379 Changes to the structure of food webs can have significant impacts on the vital rates of different species 380 or age-classes, as increasing abundance of predators or prey can increase natural mortality or increase 381 growth and survival. We identified multiple substantial changes in vital rates between the two 382 ecosystem states in Horsetooth Reservoir, driven by changes to the abundance of prey (Daphnia for age-383 0 walleye, smelt for larger size classes of walleye), competitors and predators (smelt for age-0 walleye). 384 The two ecosystem states are characterized by high adult walleye growth and survival under periods of 385 high smelt abundance. As smelt are the primary prey species for larger walleye in Horsetooth Reservoir 386 when present (Jones et al. 1994; Johnson and Goettl 1999; Lepak et al. in press), our results suggest an 387 abundance of forage allows walleye to grow from the medium to large size classes preferred by anglers, 388 and supports greater survival to maintain high abundances of large walleye. Conversely, in periods of 389 low smelt abundance, there is insufficient forage to support walleye growth from medium to large size 390 classes. These results support the findings of previous studies in which walleye growth increased 391 substantially following increases in rainbow smelt abundance (Jones et al. 1994; Fincel et al. 2014). 392 Additionally, previous research has demonstrated large walleye can become energetically constrained 393 during periods of low smelt abundance, resulting in reduced growth and increased mortality (Graeb et al. 2008). In reservoirs with limited alternative forage options, adult walleye dynamics can be tightly 394 395 coupled to the dynamics of rainbow smelt.

396

While larger walleye can benefit from abundant rainbow smelt prey, age-0 walleye are negatively
impacted by rainbow smelt through competition and predation (Johnson and Goettl 1999; Lepak et al.
2023). Smelt appear to compete with age-0 walleye for Daphnia prey, as Daphnia densities are reduced
when smelt abundance is elevated (Lepak et al. *in press*). Previous work has highlighted the changes to
zooplankton species composition and size structure following rainbow smelt establishment in
Horsetooth Reservoir (Johnson and Goettl 1999; Lepak et al. *in press*), demonstrating the patterns
expected from systems with increased abundance of efficient planktivores (Brooks and Dodson 1965).

404 Additionally, recent work has identified walleye DNA in rainbow smelt diets (Lepak et al. 2023), 405 indicating elevated smelt abundances increase the predation pressure on young walleye. While we are 406 unable to determine the relative impact of competition compared to predation, our analysis highlights 407 the strong negative impact of increased smelt abundance on the survival of age-0 walleye. Competition 408 and predation (including cannibalism) have been identified as key drivers of walleye recruitment failure 409 in other systems (Hansen et al. 1998; Chevalier 1973; Forney 1980; Mercado-Silva et al. 2007). However, 410 while high smelt abundance periods produce reduced survival of age-0 and small walleye, our model 411 also detects increased growth rates of small walleye under high smelt conditions. As walleye within our 412 small size class can already be highly piscivorous (Kolar et al. 2003; Graeb et al. 2005), periods with 413 abundant rainbow smelt may also increase the availability of energy-dense fish prey for small walleye, 414 increasing their growth rates and allowing them to transition to larger size classes. The distinct effects of 415 increased rainbow smelt abundance on different size-classes of walleye in Horsetooth Reservoir drive 416 the presence of alternative states, with implications for the ecosystem services provided by the 417 reservoir.

418

419 Walleye and rainbow smelt populations in Horsetooth Reservoir appear to comprise a life history 420 intraguild predation system, but their dynamics do not necessarily match the theoretical predictions of 421 the models. Periods of reduced rainbow smelt abundance reduce competition and predation on age-0 422 walleye (Johnson and Goettl 1999; Lepak et al. 2023; Lepak et al. in press), increasing recruitment, while 423 simultaneously reducing growth of larger walleye due to reduced prey availability. However, unlike 424 theoretical models of LHIGP, large adult walleye do not appear to be capable of maintaining sufficiently 425 low rainbow smelt abundance to promote recruitment of walleye beyond the age-0 stage while 426 simultaneously maintaining high adult biomass in Horsetooth Reservoir. While high abundances of adult 427 walleye have been demonstrated to be able to reduce rainbow smelt abundance (Krueger and Hrabik 428 2005), the effects of walleye predation on rainbow smelt populations vary among ecosystems (Kirn and 429 LaBarr 1996; Krueger and Hrabik 2005). While not explicitly incorporated into our modeling framework, 430 rainbow smelt abundance has generally declined 5-10 years after the abundance of large adult walleye 431 has increased. As adult walleye primarily prey upon smaller (< 130 mm) rainbow smelt in Horsetooth 432 Reservoir when smelt are abundant (Lepak et al. in press), these trends could indicate the presence of 433 large walleye reduces recruitment of rainbow smelt, eventually causing population declines as older 434 larger rainbow smelt individuals senesce out of the population. However, the reduction in rainbow smelt 435 ultimately drives declining abundance of large walleye due to lack of prey. As such, increasing the 436 availability and diversity of alternative prey for adult walleye may support elevated predation impacts 437 on rainbow smelt even after smelt biomass has been reduced (Mrnak et al. 2023), potentially sustaining 438 both high adult biomass and increased recruitment of walleye. However, we urge caution when 439 interpreting the impacts of walleye predation on rainbow smelt population dynamics in Horsetooth 440 Reservoir. Rather than top-down control by walleye, it is possible that rainbow smelt dynamics in 441 Horsetooth Reservoir are controlled by environmental conditions during their spawning and rearing 442 periods impacting recruitment (Feiner et al. 2015). Future studies should explicitly model the dynamics 443 of rainbow smelt population, incorporating predator-prey interactions with different life stages of 444 walleye to tease apart the drivers of not only the distinct ecosystem states detected here, but also the 445 drivers of rainbow smelt dynamics.

446

447 While we do not currently know the specific internal and external drivers controlling the dynamics of 448 rainbow smelt in Horsetooth Reservoir, the periodicity of their cycles between low and high abundance 449 states appear to be critically important to the stability and long-term trends in walleye population 450 abundance. If adult walleye are unable to effectively control rainbow smelt abundance through 451 predation and rainbow smelt abundance remains elevated, our model predicts long-term declines of 452 walleye as adult mortality is not balanced through recruitment due to competition and high predation 453 pressure on age-0 walleye. However, cyclic transitions between the two ecosystem states, like those 454 observed in the historical data, can promote long-term persistence and growth of the adult walleye 455 population, but only under certain combinations of state-specific periods. Particularly, longer periods 456 spent in the low smelt, low walleye growth state than in the high smelt, high walleye growth state 457 appear to be critical to long-term population growth for walleye. Such scenarios would involve more 458 years in which age-0 walleye are able to survive to the small size class, punctuated by shorter periods in 459 which small and medium walleye can grow to large sizes. Scenarios in which the period in the high-smelt 460 state is longer than the period in the low-smelt state are generally expected to lead to long-term 461 collapse of the walleye population. Managers can use this information to predict when stocking walleye 462 may be critical to the maintenance of the fishery, particularly if rainbow smelt numbers remain elevated 463 for long periods. Stocking walleye large enough to escape predation from rainbow smelt could mitigate 464 the impacts of the predation bottleneck on long-term walleye dynamics (Lawson and Carpenter 2014), should rainbow smelt remain abundant in the long-term. 465

467 The ability to determine both the current state and the potential for a rapid transition to an alternative 468 state from readily collected data is critically important to effective management of systems prone to 469 state shifts. Given the importance of predicting when state transitions may occur in ecosystems, there 470 has been substantial research effort into identifying statistical leading indicators of ecosystem change 471 (e.g., Carpenter and Brock 2006; Carpenter 2008; Gsell et al. 2016). However, the reliability of these 472 indicators can be limited in many systems, potentially due to insufficient temporal resolution of data or 473 not monitoring ecosystem conditions that would demonstrate early warning indicators (Burthe et al. 474 2015; Gsell et al. 2016). Yet, within well-monitored ecosystems, observations of a small number of key 475 conditions may be able to provide useful information regarding the current state of the system and 476 changes from recent states. In Horsetooth Reservoir, observations of Daphnia densities and rainbow 477 smelt abundance can inform managers about the likely state of the system before they are able to 478 observe a response in the slower dynamics of the walleye population. Historic observations suggest 479 potential threshold Daphnia densities below which the ecosystem is likely in the high adult survival state. When Daphnia density is less than 10 L^{-1} , the ecosystem is likely to be in the high smelt, high adult 480 481 survival state. As Daphnia data are logistically easier and less expensive to collect than rainbow smelt 482 densities, managers may be able to base decisions off Daphnia densities alone, though the predicted state is more uncertain the closer observed Daphnia density is to 10 L⁻¹. However, if Daphnia 483 484 observations indicate values much greater than 10 L⁻¹ or much less than 10 L⁻¹, managers could have 485 confidence in their estimate of the current ecosystem state and make management decisions 486 accordingly. For example, knowledge of the ecosystem state could inform whether and at what size to 487 stock walleye into the reservoir. During high smelt abundance periods, stocking larger fingerlings able to 488 escape predation by smelt (Lawson and Carpenter 2014) and take advantage of growth opportunities 489 from consuming smelt would be preferable to stocking walleye fry that will be subject to predation and 490 competition from smelt. Alternatively, in the low smelt abundance state recruitment to the small size 491 class occurs naturally as long as there are enough mature walleye to spawn. Therefore, stocking may not 492 be necessary under these conditions. If managers can be flexible in their ability to stock walleye into 493 Horsetooth Reservoir, conditioning stocking activities based on the ecosystem state may increase the 494 cost-effectiveness of walleye stocking efforts.

495

496 While our model is able to effectively recreate the stage-structured dynamics of the Horsetooth 497 Reservoir walleye population, several assumptions in the model require caution be taken when 498 interpreting model results. First, there are no total abundance estimates available for any life stage of 499 walleye in this system and all catch data are indices of relative abundance across time, so our estimates 500 of abundance and vital rates should also be considered relative indices. For example, there are no data 501 for age-0 walleye abundance, so we fixed the survival of this life stage in one of the ecosystem states to 502 1, and made all other stage-specific survival estimates relative to this value. As a survival rate of 1 is 503 implausible, we emphasize the need to treat all vital rate and abundance estimates as relative indices. 504 Future analyses could benefit from total abundance estimates for different stages of walleye, potentially 505 from mark-recapture methods. Additionally, while both Daphnia and rainbow smelt dynamics are key 506 components of our model and determinants of the ecosystem state, we do not explicitly account for the 507 conditions driving changes in their abundance, treating their dynamics as a random walk fit to observed 508 densities. Future research could explicitly model the population dynamics of rainbow smelt using similar 509 stage-structured or unstructured methods. Additionally, explicitly incorporating food web linkages to 510 model dynamics across three trophic levels would be a valuable avenue of future research, and could 511 identify how the food web would be expected to respond to alternative management actions (e.g., 512 changing walleye harvest rates, stocking rates, rainbow smelt control actions).

513

514 It is increasingly recognized that many exploited species undergo productivity regime shifts through time 515 (Conners et al. 2002; Vert-pre et al. 2013; Wilson et al. 2022). While the presence of alternative regimes 516 challenges management (King et al. 2015), management approaches accounting for temporal changes in 517 productivity dynamics are increasingly suggested to outperform those assuming stationary dynamics 518 (Hawkshaw and Walters 2015; Cunningham et al. 2019; Ohlberger et al. 2024), though this can depend on the specific goals of management (Bessell-Brown et al. 2024). Here, we have identified the presence 519 520 of two alternative ecosystem states controlling the growth and survival of different size classes of 521 walleye through changing food web structure in an Intermountain West reservoir system. Designing 522 future walleye management strategies (e.g., harvest regulations, stocking practices) that are flexible and 523 account for temporally dynamic walleye vital rates under shifting ecosystem states may improve the 524 long-term stability of fishery performance, allowing for both sustained recruitment and abundant adult 525 walleye preferred by anglers.

526

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- 531 References
- Abrams, P.A. 2011. Simple life history omnivory: responses to enrichment and harvesting in systems
 with intraguild predation. Am. Nat. **178**: 305–319. https://doi.org/10.1086/661243.
- Baskett, M.L., Yoklavich, M. and Love, M.S. 2006. Predation, competition, and the recovery of
 overexploited fish stocks in marine reserves. Can. J. Fish. Aquat. Sci. 63(6): 1214–1229.
- 536 https://doi.org/10.1139/f06-013.
- 537 Bessell-Brown, P., Punt, A.E., Tuck, G.N., Burch, P. and Penney, A. 2024. Management strategy
- evaluation of static and dynamic harvest control rules under long-term changes in stock
 productivity: a case study from the SESSF. Fish. Res. 273: 106972.
- 540 https://doi.org/10.1016/j.fishres.2024.106972
- Brooks, J.L. and Dodson, S.I. 1965. Predation, body size, and composition of zooplankton: the effect of a
 marine planktivore on lake plankton illustrates theory of size, competition, and predation. Science.
 150: 28–35. https://doi.org/10.1126/science.150.3692.28.
- Burthe, S.J., Henrys, P.A., Mackay, E.B., Spears, B.M., Campbell, R., Carvalho, L., Dudley, B., Gunn, I.D.M.,
 Johns, D.G., Maberly, S.C., May, L., Newell, M.A., Wanless, S., Winfield, I.J., Thackeray, S. J. and
 Daunt, F. 2016. Do early warning indicators consistently predict nonlinear change in long-term
 ecological data? J. Appl. Ecol. 53(3): 666–676. https://doi.org/10.1111/1365-2664.12519.
- Cahill, C.L., Walters, C.J., Paul, A.J., Sullivan, M.G. and Post, J.R. 2022. Unveiling the recovery dynamics of
 walleye after the invisible collapse. Can. J. Fish. Aquat. Sci. **79**(5): 708–723.
- 550 https://doi.org/10.1139/cjfas-2021-0065.
- 551 Carpenter, S.R. 2008. Emergence of ecological networks. Front. Ecol. Environ. 6(5): 228–228.
 552 https://doi.org/10.1890/1540-9295(2008)6[228:EOEN]2.0.CO;2.
- Carpenter, S.R. and Brock, W.A. 2006. Rising variance: a leading indicator of ecological transition. Ecol.
 Lett. 9(3): 311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x.
- 555 Chevalier, J. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. T. Am. Fish.
 556 Soc. 102(4): 739–744. https://doi.org/10.1577/1548-8659(1973)102<739:CAAFIF>2.0.CO;2.
- Colby, P.J., Ryan, P.A., Schupp, D.H. and Serns, S.L. 1987. Interactions in north-temperate lake fish
 communities. Can. J. Fish. Aquat. Sci. 44(S2): s104–s128. https://doi.org/10.1139/f87-314.
- 559 Conners, M.E., Hollowed, A.B. and Brown, E. 2002. Retrospective analysis of Bering Sea bottom trawl
- 560 surveys: regime shift and ecosystem reorganization. Prog. Oceanogr. **55**(1-2): 209–222.
- 561 https://doi.org/10.1016/S0079-6611(02)00079-4.

- 562 Cunningham, C.J., Anderson, C.M., Wang, J.Y.L., Link, M. and Hilborn, R. 2019. A management strategy
 563 evaluation of the commercial sockeye salmon fishery in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci.
 564 **76**(9): 1669–1683. https://doi.org/10.1139/cjfas-2018-0133.
- Denwood, M.J. 2016. runjags: an R package providing interface utilities, model templates, parallel
 computing methods and additional distributions for MCMC models in JAGS. J. Stat. Softw. **71**: 1–25.
 https://doi.org/10.18637/jss.v071.i09.
- De Roos, A.M., Schellekens, T., Van Kooten, T. and Persson, L. 2008. Stage-specific predator species help
 each other to persist while competing for a single prey. P. Natl. Acad. Sci-Biol. **105**(37): 13930–
 13935. https://doi.org/10.1073/pnas.0803834105.
- Embke, H.S., Rypel, A.L., Carpenter, S.R., Sass, G.G., Ogle, D., Cichosz, T., Hennessy, J., Essington, T.E. and
 Vander Zanden, M.J. 2019. Production dynamics reveal hidden overharvest of inland recreational
 fisheries. P. Natl. Acad. Sci-Biol. **116**(49): 24676–24681. https://doi.org/10.1073/pnas.1913196116.
- Feiner, Z.S., Bunnell, D.B., Höök, T.O., Madenjian, C.P., Warner, D.M. and Collingsworth, P.D. 2015. Nonstationary recruitment dynamics of rainbow smelt: the influence of environmental variables and
 variation in size structure and length-at-maturation. J. Great Lakes Res. 41(1): 246–258.
 https://doi.org/10.1016/j.jglr.2014.11.029.
- Feiner, Z.S., Shaw, S.L. and Sass, G.G. 2019. Influences of female body condition on recruitment success
 of walleye (*Sander vitreus*) in Wisconsin lakes. Can. J. Fish. Aquat. Sci. **76**(11): 2131–2144.
 https://doi.org/10.1139/cjfas-2018-0364.
- Fincel, M.J., Dempkowski, D.J. and Chipps, S.R. 2014. Influence of variable rainbow smelt and gizzard
 shad abundance on walleye diets and growth. Lake Reserv. Manage. **30**(3): 258–267.
 https://doi.org/10.1080/10402381.2014.914989.
- Forney, J.L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. New
 York Fish and Game Journal. 27: 105-141.
- Gaeta, J.W., Ahrenstorff, T.D., Diana, J.S., Fetzer, W.W., Jones, T.S., Lawson, Z.J., McInerny, M.C.,
 Santucci Jr, V.J. and Vander Zanden, M.J. 2018. Go big or... don't? A field-based diet evaluation of
 freshwater piscivore and prey fish size relationships. PloS one. 13(3): 0194092.
- 589 https://doi.org/10.1371/journal.pone.0194092.
- Galarowicz, T.L., Adams, J.A. and Wahl, D.H. 2006. The influence of prey availability on ontogenetic diet
 shifts of a juvenile piscivore. Can. J. Fish. Aquat. Sci. 63(8): 1722–1733. https://doi.org/10.1139/f06073.
- Gsell, A.S., Scharfenberger, U., Özkundakci, D., Walters, A., Hansson, L.A., Janssen, A.B.G., Nõges, P.,
 Reid, P.C., Schindler, D.E., Donk, E.V., Dakos, V. and Adrian, R. 2016. Evaluating early-warning

- indicators of critical transitions in natural aquatic ecosystems. P. Roy. Soc. B-Biol. Sci. 113(50):
 8089–8095. https://doi.org/10.1073/pnas.1608242113.
- Graeb, B.D., Chipps, S.R., Willis, D.W., Lott, J.P., Hanten, R.P., Nelson-Stastny, W.A.Y.N.E. and Erickson,
 J.W. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations
 in a Missouri River reservoir. In Balancing fisheries management and water uses for impounded
 river systems. American Fisheries Society, Symposium. 62: 275–292.
- Graeb, B.D., Galarowicz, T., Wahl, D.H., Dettmers, J.M. and Simpson, M.J. 2005. Foraging behavior,
 morphology, and life history variation determine the ontogeny of piscivory in two closely related
 predators. Can. J. Fish. Aquat. Sci. 62(9): 2010–2020. https://doi.org/10.1139/f05-112.
- Guill, C. 2009. Alternative dynamical states in stage-structured consumer populations. Theor. Popul.
 Biol. **76**(3): 168–178. https://doi.org/10.1016/j.tpb.2009.06.002.
- Hansen, M.J., Bozek, M.A., Newby, J.R., Newman, S.P. and Staggs, M.D. 1998. Factors affecting
 recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–1996. N. Am. J. Fish. Manage. 18: 764–
 774. https://doi.org/10.1577/1548-8675(1998)0182.0.CO;2.
- Hansen, G.J., Carpenter, S.R., Gaeta, J.W., Hennessy, J.M. and Vander Zanden, M.J. 2015. Predicting
 walleye recruitment as a tool for prioritizing management actions. Can. J. Fish. Aquat. Sci. 72(5):
 661–672. https://doi.org/10.1139/cjfas-2014-0513.
- Hansen, G.J., Midway, S.R. and Wagner, T. 2018. Walleye recruitment success is less resilient to warming
 water temperatures in lakes with abundant largemouth bass populations. Can. J. Fish. Aquat. Sci. **75**(1): 106–115. https://doi.org/10.1139/cjfas-2016-0249.
- Hawkshaw M. and Walters, C.J. 2015. Harvest control rules for mixed-stock fisheries coping with
 autocorrelated recruitment variation, conservation of weak stocks, and economic well-being. Can. J.
 Fish. Aquat. Sci. 72(5): 759–766. https://doi.org/10.1139/cjfas-2014-0212.
- Hilborn, R. and Walters, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and
 Uncertainty. Chapman and Hall. New York.
- Hin, V., Schellekens, T., Persson, L. and de Roos, A.M. 2011. Coexistence of predator and prey in
- intraguild predation systems with ontogenetic niche shifts. Am. Nat. **178**(6): 701–714.
 https://doi.org/10.1086/662676.
- Honsey, A.E., Feiner, Z.S. and Hansen, G.J. 2020. Drivers of walleye recruitment in Minnesota's large
 lakes. Can. J. Fish. Aquat. Sci. 77(12): 1921–1933. https://doi.org/10.1139/cjfas-2019-0453.
- Huss, M., Persson, L., Borcherding, J. and Heermann, L. 2013. Timing of the diet shift from zooplankton
 to macroinvertebrates and size at maturity determine whether normally piscivorous fish can persist
 in otherwise fishless lakes. Freshwater Biol. 58(7): 1416–1424. https://doi.org/10.1111/fwb.12138.

- 528 Johnson, B.M. and Goettl, J.P.Jr. 1999. Food web changes over fourteen years following introduction of
- ferror for the formation of the formatio
- 630 https://doi.org/10.1577/1548-8675(1999)019<0629:FWCOFY>2.0.CO;2.
- Jones, M.S., Goettl, J.P.Jr. and Flickinger, S.A. 1994. Changes in walleye food habits and growth following
 a rainbow smelt introduction. N. Am. J. Fish. Manage. 14: 409–414. https://doi.org/10.1577/15488675(1994)014<0409:CIWFHA>2.3.CO;2.
- King, J.R., McFarlane, G.A. and Punt, A.E. 2015. Shifts in fisheries management: adapting to regime
 shifts. Philos. T. Roy. Soc. B. **370**(1659): 20130277. https://doi.org/10.1098/rstb.2013.0277.
- Kirn, R.A. and LaBar. G.W. 1991. Stepped-oblique mid-water trawling as an assessment technique for
 rainbow smelt. N. Am. J. Fish. Manage. 11: 167–176. https://doi.org/10.1577/15488675(1991)011<0167:SOMTAA>2.3.CO;2.
- Kirn, R.A., and LaBar, G.W. 1996. Growth and survival of rainbow smelt, and their role as prey for
 stocked salmonids in Lake Champlain. T. Am. Fish. Soc. 125: 87–96. https://doi.org/10.1577/15488659(1996)125<0087:GASORS>2.3.CO;2.
- Kolar, C.S., Wahl, D.H. and Hooe, M.L. 2003. Piscivory in juvenile walleyes: relative importance of prey
 species, timing of spawning of prey fish, and density on growth and survival. T. Am. Fish. Soc.
 132(4): 679–690. https://doi.org/10.1577/T99-068.
- Krabbenhoft, C.A., Ludsin, S.A., Marschall, E.A., Budnik, R.R., Almeida, L.Z., Cahill, C.L., Embke, H.S.,
 Feiner, Z.S., Schmalz, P.J., Thorstensen, M.J. and Weber, M.J. 2023. Synthesizing professional
 opinion and published science to build a conceptual model of walleye recruitment. Fisheries. 48(4):
 141–156. https://doi.org/10.1002/fsh.10884.
- Krueger, D.M. and Hrabik, T.R. 2005. Food web alterations that promote native species: the recovery of
 cisco (*Coregonus artedi*) populations through management of native piscivores. Can. J. Fish. Aquat.
 Sci. 62(10): 2177–2188. https://doi.org/10.1139/f05-132.
- Lawson, Z.J. and Carpenter, S.R. 2014. A morphometric approach for stocking walleye fingerlings in lakes
 invaded by rainbow smelt. N. Am. J. Fish. Manage. 34(5): 998–1002.
 https://doi.org/10.1080/02755947.2014.943860.
- Lepak, J.M., Hansen, A.G., Cristan, E.T., Williams, D. and Pate, W.M. 2023. Rainbow smelt (*Osmerus mordax*) influence on walleye (*Sander vitreus*) recruitment decline: mtDNA evidence supporting the
 predation hypothesis. J. Fish Biol. **103**: 1543–1548. https://doi.org/10.1111/jfb.15523.
- Lepak, J.M., Hansen, A.G., Johnson, B.M., Battige, K., Cristan, E.T., Farrell, C.J., Pate, W.M., Roger, K.B.,
- Treble, A.J. and Walsworth, T.E., In press. Cyclical, multi-trophic-level responses to a volatile,
- introduced forage fish: learning from four decades of food web observation to inform management.Fisheries.

- Mercado-Silva, N., Sass, G.G., Roth, B.M., Gilbert, S. and Vander Zanden, M.J. 2007. Impact of rainbow
 smelt (*Osmerus mordax*) invasion on walleye (*Sander vitreus*) recruitment in Wisconsin lakes. Can. J.
- 664 Fish. Aquat. Sci. **64**: 1543–1550. https://doi.org/10.1139/f07-112.
- Mrnak, J.T., Sikora, L.W., Zanden, M.J.V. and Sass, G.G. 2023. Applying panarchy theory to aquatic
 invasive species management: a case study on invasive rainbow smelt *Osmerus mordax*. Rev. Fish.
 Sci. Aquac. **31**(1): 66–85. https://doi.org/10.1080/23308249.2022.2078951.
- Nelson, W.C. 1971. Comparative limnology of Colorado-Big Thompson project reservoirs and lakes.
 Colorado Department of Game, Fish, and Parks. Fort Collins, Colorado.
- Ohlberger, J., Schindler, D.E. and Staton, B.S. 2024. Accounting for salmon body size declines in fishery
 management can reduce conservation risks. Fish Fish. https://doi.org/10.1111/faf.12869.
- 672 Plagányi, É.E., Haywood, M.D., Gorton, R.J., Siple, M.C. and Deng, R.A. 2019. Management implications
- of modelling fisheries recruitment. Fish. Res. **217**: 169–184.
- 674 https://doi.org/10.1016/j.fishres.2019.03.007.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling.
 Proceedings of the 3rd International Workshop on Distributed Statistical Computing, March 20-22,
 Vienna, Austria. ISSN 1609-395X.
- Plummer, M. 2023. rjags: Bayesian Graphical Models using MCMC. The Comprehensive R Archive
 Network, https://cran.r-project.org/web/packages/rjags/rjags.pdf.
- Polis, G.A. and Holt, R.D. 1992. Intraguild predation: the dynamics of complex trophic interactions.
 Trends Ecol. Evol. 7(5): 151–154. https://doi.org/10.1016/0169-5347(92)90208-S.
- Post, D.M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass.
 Ecology. 84(5): 1298–1310. https://doi.org/10.1890/0012-9658(2003)084[1298:IVITTO]2.0.CO;2.
- R Core Team 2022. R: a language and environment for statistical computing. R Foundation for Statistical
 Computing, Vienna. https://www.R-project.org
- Rudstam, L.G., Parker, S.L., Einhouse, D.W., Witzel, L.D., Warner, D.M., Stritzel, J.L., Parrish, D.L. and
 Sullivan, P.J. 2003. Application of in situ target-strength estimations in lakes: examples from
 rainbow smelt surveys in Lakes Erie and Champlain. ICES J Mar. Sci. 60: 500–507.
 https://doi.org/10.1016/S1054-3139(03)00046-8.
- Schneider, J.C., and Leach, J.H. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great
 Lakes and possible causes, 1800-1975. J. Fish. Res. Board Can. **34**(10): 1878–1889.
 https://doi.org/10.1139/f77-254.
- Su, Y.S. and Yajima, M. 2022. R2jags: using R to run JAGS. The Comprehensive R Archive Network,
 https://cran.r-project.org/web/packages/R2jags/index.html.

- Szuwalski, C.S. and Hollowed, A.B. 2016. Climate change and non-stationary population processes in
 fisheries management. ICES J. Mar. Sci. **73**(5): 1297–1305. https://doi.org/10.1093/icesjms/fsv229.
- Toscano, B.J., Rombado, B.R., Rudolf, V.H.W. 2016. Deadly competition and life-saving predation: the
 potential for alternative stable states in a stage-structured predator-prey system. P. Roy. Soc. B Biol. Sci. 283(1837): 20161546. https://doi.org/10.1098/rspb.2016.1546.
- Toscano, B.J., Hin, V., and Rudolf, V.H.W. 2017. Cannibalism and intraguild predation community
 dynamics: coexistence, competitive exclusion, and the loss of alternative stable states. Am. Nat.
- 702 **190**(5): 617–630. http://dx.doi.org/10.5061/dryad.vj12j.
- Toscano, B.J. and Rudolf, V.H. 2021. Developmental change in predators drives different community
 configurations. Am. Nat. **197**(6): 719–731. https://doi.org/10.5061/dryad.d7wm37q0v.
- Van de Wolfshaar, K.E., De Roos, A.M. and Persson, L. 2006. Size-dependent interactions inhibit
 coexistence in intraguild predation systems with life-history omnivory. Am. Nat. 168(1): 62–75.
 https://doi.org/10.1086/505156.
- Vert-pre, K.A., Amoroso, R.O., Jensen, O.P. and Hilborn, R. 2013. Frequency and intensity of productivity
 regime shifts in marine fish stocks. P. Roy. Soc. B-Biol. **110**(5), pp.1779–1784.
 https://doi.org/10.1073/pnas.1214879110.
- Walters, C.J. and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment:
 implications for the theory of fishing. Can. J. Fish. Aquat. Sci. 58: 39–50.
- 713 https://doi.org/10.1139/f00-160.
- 714 Werner, E.E. and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured
- 715 populations. Annu. Rev. Ecol. S. **15**: 393–425.
- 716 https://doi.org/10.1146/annurev.es.15.110184.002141.
- Wilson, K.L., Bailey, C.J., Davies, T.D. and Moore, J.W. 2022. Marine and freshwater regime changes
 impact a community of migratory Pacific salmonids in decline. Glob. Change Biol. 28(1): 72–85.
 https://doi.org/10.1111/gcb.15895.
- 720 Zhang, F., Reid, K.B. and Nudds, T.D. 2018. Ecosystem change and decadal variation in stock–recruitment
- relationships of Lake Erie yellow perch (*Perca flavescens*). ICES J. of Mar. Sci. **75**(2): 531–540.
- 722 https://doi.org/10.1093/icesjms/fsx188.

723 Figures



Figure 1. Horsetooth Reservoir Map. The three relatively distinct basins of Horsetooth Reservoir, the
four dam structures (straight lines; three on the east and one on the north of the reservoir), and the
Hansen Feeder Canal are found on the map. Contour lines are provided in 10 m increments.








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738 Figure 3. (a-b) Observed and estimated rainbow smelt (a) and Daphnia (b) density time series. Points 739 represent observed densities, lines represent median model estimates, and light and dark grey polygons 740 represent the 95% and 50% credible intervals. (c-d) Predicted relationship between relative rainbow 741 smelt (c) and Daphnia (d) densities (1.0 represents the maximum estimated density within the time 742 series) and the probability of the ecosystem being in state 1. Lines represent median model estimates, 743 and light and dark grey polygons represent the 95% and 50% credible intervals. (e) Predicted 744 probabilities of being in ecosystem state 1 (points and error bars) and the proportion of posterior 745 samples where the population was in each ecosystem state (orange = state 1, blue = state 2) for each 746 year analyzed. Points represent the median estimate while lines extend to the 95% credible interval.



Figure 4. (a) Estimated relative abundance of age-0 walleye in the Horsetooth Reservoir population. (bd) Observed and predicted catch of different size classes of walleye. Size classes are represented by
small (150 mm - 300 mm), medium (301 mm - 451 mm), and large (> 451 mm) individuals. In all panels,
points represent observed values, lines represent median model estimates, light and dark grey polygons
represent the 95% and 50% credible intervals.



Observed Smelt Density

753

Figure 5. Predicted probability of being within each of the two ecosystem states across a range of
rainbow smelt and Daphnia densities. Orange shades represent conditions more likely to reflect
ecosystem state 1 (high age-0 survival, low growth and survival of larger walleye). Blue shades represent
conditions more likely to reflect ecosystem state 2 (low age-0 walleye survival, elevated growth and
survival of larger walleye).



Figure 6. Probability of long-term adult walleye abundance increases under different combinations of
durations for each of the two ecosystem states. Darker blue shades indicate a greater probability of
long-term walleye population growth.

RESEARCH PRIORITY:

Exploring growth and reproduction of Walleye: Using triploid and diploid walleye to explore the reproductive drain hypothesis.

OBJECTIVES

To determine if asymptotic growth in Walleye *Sander vitreus* can be attributed to mature fish allocating energy towards reproduction.

MANUSCRIPT SUBMISSION

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FULL MANUSCRIPT

Induced sterility illuminates the effects of reproduction on growth

- 2 Running Head: Does reproduction slow growth?
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18 Abstract

19 The Reproductive Drain Hypothesis is a long-held and widespread idea that the energetic costs 20 associated with reproduction drive growth deceleration in fish by appropriating energy previously 21 allocated for somatic growth prior to maturity. This theoretical notion remains contentious and has 22 been challenging to test given the difficulty of controlling reproduction in wild populations. In this study, 23 we evaluated the Reproductive Drain Hypothesis by comparing the lifetime growth of sterile (i.e., 24 triploid) walleye (Sander vitreus) with normal, fertile conspecifics co-occurring in the same ecosystem. 25 We found the Lester biphasic growth model, a model developed specifically to incorporate the 26 Reproductive Drain Hypothesis, failed to fit the growth patterns of sterile walleye (model weight = 27 0.081), and sterile walleyes were not larger than fertile ones. This evidence implies that reproduction 28 may not limit energy available for somatic growth and presents an interesting challenge to this long-held 29 concept. Alternatively, we hypothesize that individuals may increase food intake to meet the elevated 30 energetic demands associated with reproduction, and that inheritance and metabolic theory may 31 explain asymptotic growth in fish better than the Reproductive Drain Hypothesis.

32 Introduction

33 Growth and reproduction are inextricably linked, and the evolutionary trade-off between them is 34 fundamental to life history theory (Lika and Kooijman 2003; Reznick 1985; White et al. 2022). According 35 to life history theory, reproductive effort—the proportion of an organism's energy budget devoted to 36 reproductive processes—is selected for in a way that maximizes fitness, but at a cost to growth in body 37 size (Hirshfield and Tinkle 1975). In a bioenergetic context, a parallel concept, referred to as the 38 Reproductive Drain Hypothesis (RDH; Iles 1974), posits that energy is redirected from potential somatic 39 growth towards reproduction, consequently restricting overall somatic growth over an organism's 40 lifetime.

41 Reproduction's role in the energetics of individual lifetime growth of fish has been the subject of recent 42 debate (Kearney 2019; Kooijman and Lika 2014; Marshall and White 2019a, 2019b; Pauly 2019; White 43 and Marshall 2019). In fact, Pauly (2021) called the role of reproduction in lifetime growth one of the 44 most critical theoretical issues in ichthyology. This debate is centered around what is ultimately 45 responsible for driving growth deceleration in fish and other organisms that grow indeterminately. 46 Participants in this debate can generally be split into two theoretical camps, those that argue that 47 growth is shaped by the energetically intensive process of reproduction, and those that argue that 48 growth is shaped by metabolic constraints (White et al. 2022).

Several growth models (≥ 14) have been developed that are based on the principles of life history theory and have the RDH as a core assumption (reviewed by Wilson et al. 2017). Many of these models, like the Lester biphasic growth model (LBGM; Lester et al. 2004), assume that growth is biphasic, meaning that growth trajectories differ between the juvenile phase (sexually immature) and the adult phase (sexually mature). While there are biphasic models that have other biological justifications (e.g., ontogenetic shifts in diet or habitat), ones incorporating RDH are the most common (Wilson et al. 2017). In these
biphasic models, the onset of reproductive development and investment of energy towards
reproduction is responsible for the realized lifetime growth pattern (Figure 1; Lester et al. 2004).
Biphasic models with RDH at their core have outperformed uniphasic models in fitting empirical data
(Minte-Vera et al. 2016; Quince et al. 2008) and have accurately estimated age-at-maturity from the
growth trajectories of fish (Honsey et al. 2017), lending support for RDH.

However, the validity of RDH has been questioned because the synchrony between the onset of growth
deceleration and sexual maturation does not necessarily imply causation. For example, the Gill-Oxygen
Limitation Theory of Pauly (1981) supposes that reproductive development is triggered at a critical
oxygen limitation threshold, and is therefore the result, rather than the cause, of growth deceleration.
Additionally, Pauly (2019) points to the logical conundrum that female fish, which seemingly invest more
energy into reproductive development, are often larger than male conspecifics, counter to expectations
under the RDH (but see Rennie et al. 2008).

67 There are several growth models that do not assume RDH. This family of growth models are based on 68 metabolic theory and stem from the original ideas of Pütter (1920). According to metabolic theory, 69 growth is limited not by reproduction, but rather by the metabolic interplay of surface area-dependent 70 (i.e., anabolism or assimilation) and volume-dependent (i.e., catabolism or maintenance) processes 71 (Kearney 2021). The von Bertalanffy growth model (Von Bertalanffy 1938) is among the most commonly 72 used growth models in fisheries science. However, von Bertalanffy's model is essentially the same as 73 Pütter's, with a few relatively minor modifications. To acknowledge Pütter's priority (Kearney 2021), we 74 refer to this model as the Pütter-von Bertalanffy Growth Model (P-VBGM).

75 Several other models fall into the metabolic camp, including the Dynamic Energy Budget theory of 76 Kooijman (2010), the Gill-Oxygen Limitation Theory of Pauly (1981), and the Ontogenetic Growth Model 77 of West et al. (2001). Dynamic Energy Budget theory (Kooijman 2010) extends Pütter's ideas to include 78 effects of food availability, body condition, temperature, and reproduction on growth. According to 79 Dynamic Energy Budget theory, growth is modelled with strict adherence to thermodynamic principles 80 (Kearney 2021; Kooijman 2010). Rather than assuming energy is allocated according to the RDH, 81 Dynamic Energy Budget theory assumes energy is first stored in reserve then mobilized as needed for 82 different functions (Kooijman 2010). Under some assumptions, like constant food and temperature, 83 Dynamic Energy Budget theory simplifies to the P-VBGM (Kooijman 2010). The Gill-Oxygen Limitation 84 Theory is a mechanistically explicit version of the P-VBGM, in that the surface-area of gills in water-85 breathing ectotherms is what limits anabolism, and is the cause of growth deceleration (Pauly 1981). 86 The Ontogenetic Growth Model (West et al. 2001) builds on Pütter's ideas, but assumes that growth is 87 limited by supply network constraints under quarter-power, rather than third-power, scaling 88 relationships of metabolic rates (Kearney 2021).

89 In this study, we assessed RDH in a novel manner, by comparing the growth of sterile, triploid walleye 90 (Sander vitreus) to co-occurring, fertile, diploid conspecifics to examine the effects of reproductive 91 investment on lifetime growth. Like most fish species, walleye grow indeterminately (Charnov et al. 92 2001; Henderson et al. 2003). Additionally, walleyes are iteroparous, capital spawners that typically 93 spawn once per year following sexual maturation (Barton and Barry 2011; McBride et al. 2015). Triploid 94 walleyes of both sexes allocate very little, if any, energy toward the production of gametes (Figure 2) 95 and existing evidence suggests they may expend less energy on activity during the spawning period than 96 fertile diploids (Farrell et al. 2022a). Triploid female fish of other species typically show impaired gonadal 97 development (Benfey 1999; Maxime 2008), as observed for triploid female walleye (Farrell et al. 2022a).

98 However, triploid male fish of other species often exhibit similar gonadal development and reproductive 99 behavior as diploid male fish (Benfey 1999; Maxime 2008), though walleye appear to be one of a few 100 species, like common carp (Cyprinus carpio; Gervai et al. 1980) and stinging catfish (Heteropneustes 101 fossilis; Tiwary et al. 2000), where triploid males show impaired gonadal development. During the 102 walleye spawning period (i.e., mid-March to mid-April), mature diploids of both sexes exhibited much 103 higher gonadosomatic index (GSI) values than their triploid counterparts of the same age in 104 Narraguinnep Reservoir. Mean GSI for spawning diploid females was 12.6% compared to 0.4% for 105 triploid females, and mean GSI for spawning diploid males was 2.3% compared to 0.3% for triploid males 106 (Farrell et al. 2022a). Additionally, Farrell et al. (2022a) found that activity during the spawning period 107 was likely reduced for triploid male walleyes relative to diploid males, as the relative proportion of 108 triploid male walleyes caught in gillnets was much lower during the spawning period (i.e., 13% triploid to 109 87% diploid males) than outside of the spawning period, where the catch was more evenly distributed. 110 Thus, comparisons of growth patterns and body sizes between triploid and diploid walleyes cohabiting 111 under the same physical, chemical, and ecological conditions are well suited for directly testing the RDH, 112 as recently suggested by Pauly (2021).

113 We examined length-at-age data collected from sympatric fertile and sterile walleye in the context of 114 metabolic and biphasic growth under the a priori expectation of RDH. Each framework was represented 115 by a commonly used model—the P-VBGM (metabolic) and LBGM (biphasic). Our analysis encompassed 116 four phases, each with a complimentary objective. First, we used Bayesian model selection to establish 117 which framework was more suitable for characterizing the growth patterns of fertile walleye. We 118 expected the LBGM to receive greater model weight in support of the RDH, as has been shown 119 previously. Next, based strictly on the primary motivation and specification of the LBGM, we outlined 120 expected growth patterns for sterile walleye in the absence of reproduction, and simplified the LBGM

121 accordingly by removing the post-maturation phase. Model fitting procedures were repeated to assess 122 whether length-at-age for sterile walleye aligned with theoretical expectations, and to facilitate general 123 comparisons of growth patterns between sterile and fertile conspecifics. Acknowledging that numerous 124 interacting factors may slow growth, patterns for sterile walleye could resemble fertile walleye. 125 However, sterile fish are still expected to achieve greater maximum body size due to energetic cost 126 savings under the RDH (ceteris paribus). We explored this notion by finding the probability that sterile 127 walleye were larger than fertile walleye of the same age and discuss important caveats of our analyses 128 to stimulate further research. Lastly, we fit the full LBGM, allowing the model fitting process to estimate 129 the theoretical age-at-maturity (Honsey et al. 2017), to sterile walleye length-at-age data to explore if 130 biphasic growth patterns dictated by phenomena other than RDH may still be appropriate for explaining 131 the growth of sterile walleye.

132 Methods

133 Narraguinnep Reservoir (Latitude: 37.49°N, Longitude: 108.62°W) is a 215-ha reservoir located within 134 the upper Colorado River basin in southwest Colorado, USA. Sportfish management in the upper 135 Colorado River basin utilizes several strategies to support the recovery of threatened and endangered 136 fish, which includes the stocking of sterile nonnative piscivores. Walleyes were first introduced to 137 Narraguinnep Reservoir in 1973, and stocking occurred sporadically (1973, 1975-1979, 1988, 1992, 138 1998-2000, 2002, 2004, 2006; Colorado Parks and Wildlife, unpublished data) prior to the initiation of 139 the sterile walleye stocking program in 2008. In an effort to continue to provide a sought-after 140 sportfishing opportunity while mitigating the risk of natural and illegal dispersal of reproductively 141 capable individuals that could harm downstream native species recovery efforts (Fetherman et al. 2015; 142 Farrell et al. 2022a), Colorado Parks and Wildlife began stocking Narraguinnep Reservoir with sterile 143 triploid walleye in 2008. Triploid walleyes stocked in Narraguinnep Reservoir were produced via 151

144 hydrostatic pressure shocks (Fetherman et al. 2015), and stockings occurred regularly (2008, 2010-2018, 145 2021-2022; Colorado Parks and Wildlife, unpublished data). Because complete (i.e., 100%) induction of 146 triploidy in walleye is rare (Hansen et al. 2023a), the current policy for stocking triploid walleye in the 147 upper Colorado River basin allows for the stocking of triploid walleyes at a minimum induction rate of 148 95% (Upper Colorado River Recovery Program 2022). Additionally, because natural recruitment of 149 walleye in Colorado reservoirs is thought to be limited (Finnell 1982), coupled with lower post-stocking 150 survival rates of triploid walleye relative to diploid walleye (Farrell et al. 2024), fertile diploids in this 151 system are likely the result of incomplete induction of triploidy, and genetically related to triploids of the 152 same cohort. Furthermore, all walleyes stocked in Narraguinnep Reservoir have primarily been sourced 153 from the same broodstock (Ken Kehmeier, Colorado Parks and Wildlife, personal communication). As a 154 result, Narraguinnep Reservoir contains a population of fertile and sterile walleyes of a wide range of 155 sizes and ages that presented a unique opportunity to assess the RDH.

156 Walleyes were collected with Fall Walleye Index Netting (FWIN) gillnets periodically from 2018 to 2021. 157 Sampling occurred every spring (March 19 – April 5 2018; March 18 – 29 2019; March 15 – 19 2020; 158 April 11 - 152021) to coincide with the spawning period for walleye, during the summer in three years 159 (July 17 – 19 2018; June 10 – 13 2019; July 19 – 21 2021), and during the fall in two years (October 15 – 18 2020; October 17 – 18 2021). Gillnets were 1.8m deep by 61.0 m long consisting of 8 mesh sizes (25, 160 161 38, 51, 64, 76, 102, 127, 152 mm stretch measure) constructed with monofilament (Morgan 2002). Our 162 catch was likely biased against walleyes <300mm. Size-dependent retention coefficients estimated by 163 Walker et al. (2013) and Hansen et al. (2023b) for FWIN gillnets were approximately 0.5 for walleyes 164 around 140 mm total length (TL), values then increased linearly to near 1.0 until walleyes reached 300 165 mm TL, and were ≥ 0.9 for walleyes >300 mm TL. We recorded TL for each individual. Sex and maturity 166 were determined by internal, macroscopic examination of gonads and classified according to Duffy et al. 167 (2000). Differntiating sexual characteristics include length, shape, and symmetry of the gonads, as well
168 as the placement of the dorsal blood vessel, and maturity was determined by the translucency of the
169 gonads and/or prescence of gametes. We collected blood and/or fin tissue samples to determine ploidy
170 using methods described in Farrell et al. (2022b). All sampling procedures were approved by the
171 Colorado State University Institutional Animal Care and Use Committee (Protocol # 18-7822A).

172 We estimated the age of walleyes using sagittal otoliths (Long and Grabowski 2017). Otoliths were 173 embedded in epoxy and sectioned transversely through the core, photographed using a camera 174 mounted to a compound microscope at 40 – 100x magnification under reflected light. An experienced 175 reader (author CJF) aged each fish, blind to size, ploidy, and sex, three times using the RFishBC package 176 in R (Ogle 2019). Fish were assigned fractional ages for each otolith read, which was calculated as the 177 time elapsed in years from hatch until capture, assuming fish hatched on April 1st of their estimated 178 hatch year. Ageing replicates were incorporated into hierarchical Bayesian fits of growth models to 179 incorporate observation uncertainty into parameter estimates (Cope and Punt 2007).

All statistical analyses were performed using R 4.1.3 (R Development Core Team 2022). We used package brms to fit the nonlinear growth models in a hierarchical Bayesian framework (Bürkner 2017, 2018, 2021). This package is a high-level interface to Stan that allows users to specify hierarchical Bayesian models using formula syntax that is similar to package lme4, a popular package used to fit frequentist mixed models in R (Bates et al. 2015). The package loo (Vehtari et al. 2017; Yao et al. 2018) was used to perform leave-one-out cross validation to compute model weights for model comparison. Figures were created using packages ggplot2 (Wickham 2016) and tidybayes (Kay 2022).

187 We characterized length-at-age for each sex and ploidy group using both the P-VBGM and the LBGM.

188 Both models were fit independently for each ploidy, resulting in a total of four models. Ageing error was

incorporated in parameter estimates by using a random effect of otolith reading (Cope and Punt 2007).

190 We used the Beverton and Holt (1957) parameterization of the P-VBGM to represent the metabolic

191 growth framework. Below is a semi-formal model specification for the P-VBGM implemented in brms:

192
$$y_i \sim lognormal(\mu_{ij}, \sigma)$$
 (1)

193
$$\mu_{ij} = \log\left(L_{\infty i}\left(1 - e^{-k_i\left(t_i - t_{0_i}\right)}\right)\right) \text{ for } j = 1, 2, 3$$
(2)

$$L_{\infty_i} \sim sex + (1|reading) \tag{3}$$

195
$$K_i \sim sex + (1|reading) \tag{4}$$

$$t_{0_i} \sim sex + (1|reading) \tag{5}$$

197 $\sigma \sim 1$ (6)

198 where y_i is TL at fractional age t for sex-by-ploidy group i and otolith reading j, L_{∞} is the mean asymptotic 199 TL, K is the Brody growth coefficient, t_0 is the theoretical age at zero length, and (1|*reading*) is the 200 random effect of otolith reading. The lognormal distribution was used to represent length-at-age 201 because length is strictly positive. We used uniform priors for L_{∞} , K, t_0 and σ . Because L_{∞} , K, and σ are 202 strictly positive, the lower bound of the uniform prior for these parameters was zero. We set the upper 203 bound for L_{∞} to 1041 mm, which corresponds to the largest recorded walleye length (Gabelhouse 1984). 204 We set the upper bound for K to 5, far greater than most estimates of K for walleye, which rarely 205 exceeds 1 (Quist et al. 2003). Similarly, we set conservative bounds for t_0 ranging from -3 to 3 (Quist et 206 al. 2003). For σ , we set an upper bound of 7 to allow enough variation within the distribution so that it 207 covered the largest recorded walleye length (Gabelhouse 1984).

208 According to theory underlying P-VBGM, growth is constrained metabolically:

$$L_{\infty} = \frac{f\{\dot{k}_{am}\}}{[\dot{k}_{C}]} \tag{7}$$

210
$$k = \frac{\left[\dot{k}_C\right]}{3} \tag{8}$$

211
$$f = \frac{[\dot{k}_N]}{[\dot{k}_N] + [\dot{k}_M]}$$
(9)

where *f* is the scaled functional response, $\{\dot{k}_{am}\}$ is maximum specific nutrient concentration for anabolism rate, $[\dot{k}_{C}]$ is the specific catabolic rate, $[\dot{k}_{N}]$ is the specific nutrient diffusion coefficient, and $[\dot{k}_{M}]$ is the specific basal metabolic rate (or standard metabolic rate; Chabot et al. 2016), with dots indicating rates, square brackets indicating volume-specific quantities, and curly brackets indicating surface-area quantities (Kearney 2021).

We chose the LBGM (Lester et al. 2004) to represent the biphasic growth framework motivated by
reproductive drain because of its prevalence in the fisheries literature, similarity to other biphasic
growth models, and relative simplicity and ease of fitting (Lester et al. 2014; Wilson et al. 2017). Below is
a semi-formal model specification for the LBGM implemented in brms:

221
$$y_i \sim lognormal(\mu_{ij}, \sigma)$$
 (10)

222
$$\mu_{ij} = \begin{cases} h_i(t_j - t_{1_i}) \text{ when } t \leq T \text{ for } j = 1,2,3\\ L_{\infty_i} \left(1 - e^{-K_i [t - t_{0_i}]} \right) \text{ when } t > T \text{ for } j = 1,2,3 \end{cases}$$
(11)

$$t_{1_i} \sim sex + (1|reading) \tag{12}$$

$$h_i \sim sex + (1|reading) \tag{13}$$

where *h* is the maximum growth rate (length per unit time), t_1 and t_0 are the hypothetical ages at zero length for the juvenile and adult portions of the model, respectively, and *T* is the age when allocation of energy to reproduction begins, one year prior to age-at-50% maturity (Lester et al. 2004). We used the same priors for L_{∞} , *K*, t_0 , and σ as we did for the P-VBGM fits (equations 3 – 5). We used a flat prior for t_1 and a uniform prior for *h* that conservatively encompassed the fastest documented growth rates for juvenile walleye (Bozek et al. 2011). We estimated *T* for diploids by:

$$T = -\frac{c}{d} - 1 \tag{14}$$

where *c* and *d* are the intercept and slope of the logistic maturity-at-age regression:

$$logit(p) = c + dt$$
(15)

where *p* is the probability of maturity at age *t* and $-\frac{c}{d}$ is the age-at-50% maturity (Chen and Paloheimo 1994).

According to LBGM's underlying theory, growth is constrained by the energetic costs associated withreproduction:

$$L_{\infty} = \frac{3h}{g} \tag{16}$$

$$k = \ln\left(1 + \frac{g}{3}\right) \tag{17}$$

where g is the annual physical investment in reproduction (i.e.,
$$g = \text{gonad weight/somatic weight}$$
). Since

- 241 sterile walleyes do not develop mature gonads nor appear to devote energy to other reproductive
- activities (i.e., *g* = 0; Farrell et al. 2022a), we would expect their growth patterns to remain
- 243 predominantly linear over the lifespan of fertile conspecifics under the assumptions of the LBGM (Figure

244 1). We evaluated corresponding model residuals to explore congruence between observed data for 245 sterile fish and theoretical expectations. Each model was fit by implementing three chains of length 246 10,000 using brms and the No-U-Turn sampler, which eliminates the need to define the 'number-of-247 steps' parameter required for Hamiltonian Monte Carlo sampling (Hoffman and Gelman 2014). For each 248 chain, the first 1,000 iterations were discarded as burn-in, leaving 27,000 draws to make inference on 249 the posterior distribution of each model's parameters. Convergence of chains was assessed by 250 examining traceplots and using the scale reduction factor \hat{r} , with estimates less than 1.05 considered 251 acceptable (Gelman and Rubin 1992).

We used leave-one-out cross validation (Vehtari et al. 2017) for model comparison. We used leave-one-out cross validation because penalization based on the number of parameters would bias model
comparisons against the LBGM, as it has two more parameters than the P-VBGM (Vehtari et al. 2017).
Fertility-specific model weights were computed using the stacking method (Yao et al. 2018). Stacking
computes model weights by combining all models and maximizing the leave-one-out predictive density
of the combination distribution and has been shown to outperform other model averaging methods
(Yao et al. 2018).

For the third phase of the analysis, we examined how the body size of sterile walleye compared to fertile walleye. According to the expectations of RDH, it is expected that sterile walleye would be larger than fertile walleye, due to differences in reproductive development. We used 1,000 draws from the posterior fits of the P-VBGM from age-0 to age-14 (bin size = 0.1) to find the sex-specific probability that sterile walleyes were larger than fertile walleyes.

For the fourth phase of the analysis, we fit the full LBGM to sterile walleye, allowing for the model to estimate *T* (Honsey et al. 2017; Wilson et al. 2017) and compared the fit of the LBGM to that of the P-

VBGM in the same manner as we did in phase two of our analysis. The modelling in this phase was conducted the same as we did in phase two for fertile fish, except that *T* was estimated during the model fitting process using age-at-length data, as opposed to phase two where *T* was estimated using a logistic maturity-at-age regression. We calculated *g* for sterile walleyes by rearranging equation 16 to compare with estimates for fertile walleye calculated from parameter posteriors estimated in phase two.

272 Results

273 Overall, 891 individuals were included in our analysis. Fertile females (*n* = 233) ranged in age from 0.5–

13.3 years old, and TL from 183–692 mm. Sterile females (*n* = 195) ranged in age from 1.5–11.0 years

old, and TL from 259–578 mm. Fertile males (*n* = 348) ranged in age from 0.5–13.3 years old, and TL

from 179–593 mm. Sterile males (*n* = 115) ranged in age from 2.2–12.6 years old, and TL from 248–503
 mm (Figure 3).

278 The first phase of our analysis asked which growth framework was more suitable for describing the 279 asymptotic growth patterns of fertile walleye. Parameter estimates for the logistic regression were c = -280 5.86 (σ = 0.87) and d = 1.3 (σ = 0.19) for females, and c = -6.52 (σ = 1.05) and d = 2.26 (σ = 0.33) for 281 males. Correspondingly, estimates of T were 3.51 (σ = 0.20) for females and 1.88 (σ = 0.12) for males. 282 While both the P-VBGM (Table 1) and LBGM (Table 2) fit length-at-age data for fertile walleye well 283 (Figures 4 and 5), model selection indicated that the LBGM (model weight = 0.576) described the data 284 for fertile walleye somewhat better than the P-VBGM (model weight = 0.424). This aligned with previous 285 work showing that biphasic models outperform uniphasic ones for fertile fish (Minte-Vera et al. 2016; 286 Quince et al. 2008).

287 The second phase of our analysis compared the growth patterns of sterile walleye to theoretical 288 expectations in the absence of reproduction to explore the degree of congruence with assumptions 289 intrinsic to the LBGM. Counter to expectations under RDH, the growth patterns of sterile walleye closely 290 resembled fertile walleye and were not predominately linear over the full age-range examined (Figure 4 291 and 5). Residuals for both approaches to fitting the LBGM to sterile walleye demonstrated strong over-292 estimation of length for older age-classes (Figure 5). This violation of assumptions was reflected in the 293 poor model weight estimated for the LBGM (0.081) compared to the P-VBGM (0.919) for sterile walleye. 294 The third phase of our analysis compared the expected age-specific sizes of fertile and sterile walleye 295 with the expectation that, following the maturity of fertile walleye, sterile fish should be larger to 296 support RDH. However, we found little evidence to support this expectation (Figure 6). Over the span of 297 ages considered (0–14 years), we found that the probability sterile fish were larger than fertile fish was

fertile fish reached *T* (3.51 years). For males, this probability was highest at *T* (p = 0.006). Estimates of L_{∞} for the P-VBGM were less for sterile than fertile walleye within each sex, but females were larger than males regardless of fertility (Table 1, Figure 7).

<0.10. For females, the highest probability occurred at t=0 and decreased with age and was \leq 0.025 after

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302 The fourth and final phase of our analysis examined how the LBGM compared to the P-VBGM for sterile 303 fish when we allowed the LBGM to estimate T. The estimated means and standard deviations of the 304 posterior distributions of T were 3.06 (σ = 0.44) for sterile females and 2.32 (σ = 0.62) for sterile males, 305 and overlapped with estimates of T for fertile walleyes of the same sex (Table 2, Figure 8). Model 306 selection showed that the LBGM (model weight = 0.819) vastly outperformed P-VBGM (0.181) in this 307 phase of the analysis. For females, the posterior distribution of g was 0.344 (σ = 0.017) for fertile 308 females and 0.297 (σ = 0.136) for sterile females. For males, the posterior distribution of q was 0.688 (σ 309 = 0.029) for fertile males and was 1.26 (σ = 0.440) for sterile males.

310 Discussion

311 Our findings indicate that reproduction may not drive growth deceleration, contrary to what is expected 312 under the RDH. While the LBGM, a model with RDH as a key motivation, received more model weight 313 than the P-VBGM for fertile fish as has been previously demonstrated (Quince et al. 2008; Minte-Vera et 314 al. 2016), it could not characterize the asymptotic nature of body size observed for sterile walleye that 315 invest little to no energy into reproduction. The LBGM represented the growth patterns of sterile 316 walleye poorly, as it received only 8.1% of model weight in contrast to 91.9% received by the P-VBGM. 317 Furthermore, under the RDH, we expected estimated sizes for sterile walleye to exceed fertile walleye. 318 Instead, the probability that sterile walleye were larger (by at least 5%) than post-mature fertile walleye 319 of the same age was less than 0.006. Lastly, sexual size dimorphism, a pattern typical for a multitude of 320 species including walleye, was also exhibited by sterile walleye, suggesting that adult body sizes may be 321 the outcome of evolutionary pressures to maximize reproductive output with minimal parental care 322 (Bozek et al. 2011; Hirshfield and Tinkle 1975). This evidence suggests that [1] growth trajectories of 323 sterile fish may likely be better explained by a combination of inheritance and metabolic theory (White 324 et al. 2022), and [2] reproduction, rather than causing growth deceleration, may stimulate food 325 consumption to compensate for its costs.

Inheritance and metabolic theory may better explain growth of sterile fish because models constructed on the foundation of RDH fail to recreate their non-linear growth trajectory. Contrary to expectations of RDH, sterile, triploid walleyes exhibited asymptotic growth. This does not mean biphasic models are unable to describe the growth of sterile fish. When we allowed the LBGM to estimate *T* for sterile fish in the fourth phase of our analysis, the LBGM received 81.9% of the model weight, compared to 18.1% for the P-VBGM. However, because sterile walleyes invest little to no energy in reproduction (Farrell et al. 2022a), the mechanism for their asymptotic growth pattern is not due to investment in reproduction but could be due to phenomena motivating other biphasic models such as changes in growth patterns with
age, diet shifts, or habitat shifts (Wilson et al. 2017). Furthermore, we are not suggesting that
reproduction does not play a role in shaping growth over evolutionary timescales as predicted by life
history theory. In fact, we believe the similarity of growth for fish of the same sex regardless of fertility,
and the conservation of sexual size dimorphism in sterile walleyes, indicate that growth likely has a
strong genetic basis and is inherited, and as such subjected to evolutionary pressures and metabolic
constraints (White et al. 2022)

Instead of limiting growth, our evidence suggests that reproduction may be an additional cost that must be met by increasing food intake, a possibility previously hypothesized by Trippel et al. (2014) to explain similarities in growth between fertile and sterile Atlantic cod (*Gadus morhua*). Dynamic Energy Budget theory reduces to the P-VBGM under the assumption of constant temperature and food availability:

$$L_{\infty} = \frac{\kappa f\{\dot{p}_{Am}\}}{[\dot{p}_{M}]}$$
(18)

345 where κ is the fraction of energy spent on maintenance plus somatic growth, f is the scaled functional response $(f = \frac{X}{X + K}, X = \text{food density}, K = \text{half saturation coefficient}), {<math>\dot{p}_{Am}$ } is the surface-area-346 specific maximum assimilation rate, and $[\dot{p}_M]$ is the specific volume-linked somatic maintenance rate 347 348 (Kooijman 2010). While we lack information regarding the metabolism of triploid walleye, triploid fish 349 generally have similar metabolic rates as diploid conspecifics in optimal conditions (Benfey 1999; 350 Maxime 2008), but may be imparied in sub-optimal environments, particularly those with high water 351 temperatures and/or low oxygen levels, as has been observed for Salmonines (Ojolick et al. 1995; Fraser 352 et al. 2012; Hansen et al. 2015; Sambrus et al. 2017; Riseth et al. 2020; Jensen and Benfey 2022). 353 Maximum daily averaged bottom water temperatures in Narraguinnep Reservoir from 2019-2021 354 (measured with Onset HOBO Pendant UA-002-08 temperature loggers) were 17.7°C in 2019, 20.0°C in

355 2020, and 21.0°C in 2021 (Figure 9), all below the optimal temperature for consumption for diploid 356 walleye (22.6°C; Hokanson 1977). Thus, if triploid walleyes exhibit impaired high-temperature tolerance, 357 it likely had a limited effect on walleyes in this study. If $\{\dot{p}_{Am}\}$ and $[\dot{p}_{M}]$ are similar for diploid and 358 triploid walleye, the fraction of energy spent on reproductive development and maturity maintenance 359 (i.e., $1 - \kappa$) is proportional to feeding. If reproductive investment is proportional to feeding as we 360 hypothesize, growth models such as Dynamic Energy Budget theory and the Ontogenetic Growth Model 361 can easily accommodate reproductive hyperallometry (Barneche et al. 2018), calling the necessity for 362 new growth models into question (Kearney 2019; Marshall and White 2019a; Sadoul et al. 2020). 363 There is evidence to support the hypothesis that fertile walleye in this system increase food intake to 364 meet the energetic demands of reproduction. Food consumption is the primary pathway of mercury 365 uptake in fish (Hall et al. 1997), and mercury concentrations have been used to reconstruct food 366 consumption rates (Trudel et al. 2000). Farrell et al. (2022a) found that mature fertile walleye from the 367 same population examined here had significantly higher (by 20.3-37.5%) somatic mercury 368 concentrations than sterile walleye of the same age, despite each group having similar diet compositions 369 and experiencing the same thermal conditions. Using a bioenergetics approach, they estimated that 370 fertile walleyes required approximately 32% higher food consumption rates than sterile walleyes to 371 support heightened levels of reproductive investment (Farrell et al. 2022a). 372 While assessments of sterile conspecifics are useful for examining the effects of reproduction and

374 sterility is induced via triploidy. Though we assume that the fertile diploids included in this analysis were

maturity on a wide variety of response variables, such comparisons are not without complications when

375 likely the result of incomplete induction of triploidy, and genetically related to triploids of the same

376 cohort, we cannot rule out that a naturally reproducing population of walleye may have been

373

377 established in Narraguinnep Reservoir following their introduction. Thus, fertile diploids in this study

378 may have been subjected to selective pressures over several generations and could be a factor 379 contributing to the growth patterns we observed. Additionally, triploids have 50% more DNA than 380 diploids and therefore larger cells to maintain the ratio of nuclear to cytoplasmic volume (Benfey 1999). 381 This means that triploid cells have a smaller surface area to volume ratio compared to diploids, which 382 could affect processes limited by surface area, like oxygen uptake (Pauly 1981). However, disadvantages 383 associated with a smaller surface area to volume ratio may be offset by the fact that triploids have fewer 384 cells, thus decreasing overall maintenance costs (Benfey 1999; Maxime 2008; Piferrer et al. 2009). 385 Likewise, triploidy affects hematology in complex ways, which could affect respiratory efficiency (Benfey 386 1999). It appears that changes in cell size and hematology for triploids are compensated for since 387 metabolism, aerobic capacity, and other physiological processes remain similar between ploidies 388 (Benfey 1999; Maxime 2008; Piferrer et al. 2009). Further work on triploid walleye addressing 389 metabolism, assimilation, and maintenance costs, and how these processes compare to diploid walleye, 390 particularly in larger fish, is needed to support or refute our conclusions. Alternatively, germ cell 391 elimination is a promising new technique for producing sterile fish that do not have the cytological 392 complications of triploids (Zohar 2021). Comparisons using fish sterilized in this way should also be 393 useful for studying the potential tradeoff between growth and reproduction. Furthermore, the 394 generality of our findings should be tested with comparisons of sterile and fertile conspecifics using 395 species and taxa with different life history strategies (Winemiller and Rose 1992).

Our findings call into question the validity of the RDH and its relevance for mechanistic descriptions of fish growth. Metabolically-based growth models, like Dynamic Energy Budget theory, the Ontogenetic Growth Model, and the Gill-Oxygen Limitation Theory, do not assume that reproduction hampers growth in body size (Kearney 2021), and may be more appropriate for describing patterns of indeterminate growth. Because survival and reproductive output are highly size-dependent in fishes 401 (Barneche et al. 2018; Ebenman and Persson 1988), interpreting differences in life history strategies and
402 predicting the fitness-related consequences of rapid environmental change require a mechanistic
403 understanding of the hierarchy of energy allocation. By refining our understanding of growth from a
404 mechanistic perspective, we will be more able to accurately predict and interpret the effects of
405 perturbations such as climate change, exploitation, pollution, invasive species, and habitat degradation
406 on growth and population dynamics.

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416 **Conflict of Interest**

417 The authors declare no conflicts of interest.

418 Author Contribution Statement

- 419 Conceptualization: Collin Farrell, Adam Hansen, Brett Johnson
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- 427 Christopher Myrick
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431 Data Availability

- 432 Data generated and analyzed during this study are available from the corresponding author upon
- 433 reasonable request.

434 **References**

- 435 Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. 2018. Fish reproductive-
- 436 energy output increases disproportionately with body size. Science, 360(6389): 642-645.
- 437 https://doi.org/10.1126/sciences.aao6868.
- 438 Barton, B. A., and Barry, T. P. 2011. Reproduction and environmental biology. *In* Biology,
- 439 management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries
- 440 Society, Bethesda, Md. pp. 199-232. https://doi.org/10.47886/9781934874226.ch6.
- 441 Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models
- 442 using lme4. J. Stat. Softw. 67(1): 1-48. https://doi.org/10.18637/jss.v067.i01.
- Benfey, T. J. 1999. The physiology and behavior of triploid fishes. Rev. Fish. Sci. 7(1): 39-67.
- 444 https://doi.org/10.1080/10641269991319162.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery
- 446 Investigations (Great Britain, Ministry of Agriculture, Fisheries, and Food), London.
- 447 https://doi.org/10.1007/978-94-011-2106-4.
- Bozek, M. A., Baccante, D. A., and Lester, N. P. 2011. Walleye and sauger life history. In Biology,
- 449 management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries
- 450 Society, Bethesda, Md. pp. 233-302. https://doi.org/10.47886/9781934874226.ch7.
- 451 Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. J. Stat.
- 452 Softw. 80(1): 1-28. https://doi.org/10.18637/jss.v080.i01.
- 453 Bürkner, P.-C. 2018. Advanced Bayesian multilevel modeling with the R package brms. The R
- 454 Journal, 10(1): 395-411. https://doi.org/10.32614/rj-2018-017.

- 455 Bürkner, P.-C. 2021. Bayesian item response modeling in R with brms and Stan. J. Stat. Softw.
- 456 100(5): 1-54. https://doi.org/10.18637/jss.v100.i05.
- 457 Chabot, D., D. J. McKenzie, J. F. Craig. 2016. Metabolic rate in fishes: definitions, methods and
- 458 significance for conservation physiology. J. Fish Biol. 88(1): 1-9.
- 459 https://doi.org/10.1111/jfb.12873.
- 460 Charnov, E. L., Turner, T. F., and Winemiller, K. O. 2001. Reproductive constraints and the
- 461 evolution of life histories with indeterminate growth. P. Natl. Acad. Sci. Biol. 98(16): 9460-
- 462 9464. https://doi.org/10.1073/pnas.161294498.
- 463 Chen, Y., and Paloheimo, J. E. 1994. Estimating fish length and age at 50% maturity using a
- 464 logistic type model. Aquat. Sci. 56(3): 206-219. https://doi.org/10.1007/BF00879965.
- 465 Cope, J. M., and Punt, A. E. 2007. Admitting ageing error when fitting growth curves: an
- 466 example using the von Bertalanffy growth function with random effects. Can. J. Fish. Aquat.
- 467 Sci. 64(2): 205-218. https://doi.org/10.1139/F06-179.
- 468 Deslauriers, D, Chipps, S. R., Breck, J. E., Rice, J. A., and Madenjian, C. P. 2017. Fish
- Bioenergetics 4.0: An R-based modeling application. Fisheries 42(11): 586-596.
- 470 https://doi.org/10.1080/03632415.2017.1377558.
- 471 Duffy, M. J., McNulty, J. L., and Mosindy, T. E. 2000. Identification of sex, maturity, and gonad
- 472 condition of walleye (*Stizostedion vitreum vitreum*). Northwest Science and Technology Field
- 473 Guide No. FG-05, Thunder Bay. Ontario Ministry of Natural Resources, Northwest Region
- 474 Science and Technology Unit, Thunder Bay.
- 475 Ebenman, B., and Persson, L. 1988. Size-structured populations: ecology and evolution.
- 476 Springer, Berlin. https://doi.org/10.1007/978-3-642-74001-5.

- 477 Farrell, C. J., Johnson, B. M., Hansen, A. G., and Myrick, C. A. 2022a. Induced triploidy reduces
- 478 mercury bioaccumulation in a piscivorous fish. Can. J. Fish. Aquat. Sci. 79(2): 200-215.
- 479 https://doi.org/10.1139/cjfas-2021-0037.
- 480 Farrell, C. J., Johnson, B. M., Hansen, A. G., Myrick, C. A., Anderson, E. C., Delomas, T. A.,
- 481 Schreier, A. D., and Van Eenennaam, J. P. 2022b. Cytological and molecular approaches for
- 482 ploidy determination: results from a wild walleye population. N Am. J. Fish. Manage. 42(4):

483 849-856. https://doi.org/10.1002/nafm.10771.

- 484 Farrell, C. J., Hansen, A. G., Brandt, M. M., Myrick, C. A., and Johnson, B. M. 2024. An evaluation
- of the relative size, body condition, and survival of triploid Walleye in the wild. N. Am. J. Fish.
- 486 Manage. 44(1):172-188. https://doi.org/10.1002/nafm.10972.
- 487 Fetherman, E. R., Lepak, J. M., Brown, B. L., and Harris, D. J. 2015. Optimizing time of initiation
- 488 for triploid walleye production using pressure shock treatment. N. Am. J. Aquacult. 77(4):

489 471-477. https://doi.org/10.1080/15222055.2015.1040568.

- 490 Finnell, L. 1982. Walleye studies. (Project F-4-R, Final Report). Colorado Division of Wildlife,
- 491 Federal Aid in Fish Restoration. Denver.
- 492 Fraser, T. W. K., Fjelldal, P. G., Hansen, T., and Mayer, I. 2012. Welfare coonsiderations of
- 493 triploid fish. Rev Fish Sci 20(4): 192-211. https://doi.org/10.1080/10641262.2012.704598.
- 494 Gabelhouse, D. W. 1984. A length-categorization system to assess fish stocks. N. Am. J. Fish.
- 495 Manage. 4(3): 273-285. https://doi.org/10.1577/1548-8659(1984)4<273:ALSTAF>2.0.CO;2.
- 496 Gelman, A., and Rubin, D. B. 1992. Inference from iterative simulation using multiple
- 497 sequences. Stat. Sci. 7(4): 457-472. https://doi.og/10.1214/ss/1177011136.

- 498 Gervai, J., Peter, S., Nagy, A., Horvath, L., and Csanyi, V. 1980. Induced triploidy in carp, Cyprinus
- 499 *carpio* L. J. Fish Biol. 17(6): 667-671 https://doi.org/10.1111/j.1095-8649.1980.tb02800.x.
- Hall, B. D., Bodaly, R. A., Fudge, R. J. P., Rudd, J. W. M., and Rosenberg, D. M. 1997. Food as the
- 501 dominant pathway of methylmercury uptake by fish. Wat. Air and Soil Poll. 100(1-2): 13-24.
- 502 https://doi.org/10.1023/a:1018071406537.
- 503 Hansen, A. G., C. J. Farrell, and B. M. Johnson. 2023a. Simulated effects of imperfect sterile
- sport fish stocking on persistence of fertile fish in new exploited populations. N. Am. J. Fish.
- 505 Manage. 43(4): 908-934. https://doi.org/10.1002/nafm.10926.
- Hansen, A. G., Miller, M. W., Cristan, E. T., Farrell, C. J., Winkle, P., Brandt, M. M., Battige, K. D.
- and Lepak., J. M. 2023b. Gill net catchability of walleye (Sander vitreus): Are provincial
- 508 standards suitable for estimating adult density outside the region? Fish Res. 266.
- 509 https://doi.org/10.1016/j.fishres.202.106800.
- Hansen, T. J., Olsen, R. E., Stein, L., Oppedal, F., Torgersen, T., Breck, O., Remen, M., Vågseth, T.,
- and Fjelldal, P. G. 2015. Effect of water oxygen level on performance of diploid and triploid
- 512 Atlantic salmon post-smolts reared at high temperature. Aquaculture 435(1): 354-360.
- 513 https://doi.org/10.1016/j.aquaculture.2014.10.017.
- Henderson, B. A., Collins, N., Morgan, G. E., and Vaillancourt, A. 2003. Sexual size dimorphism
- of walleye (*Stizostedion vitreum vitreum*). Can. J. Fish. Aquat. Sci. 60(11): 1345-1352.
- 516 https://doi.org/10.1139/f03-115.
- 517 Hirshfield, M. F., and Tinkle, D. W. 1975. Natural selection and the evolution of reproductive
- 518 effort. Proc. Nat. Acad. Sci. USA. 72(6): 2227-2231.
- 519 https://doi.org/doi:10.1073/pnas.72.6.2227.

- 520 Hoffman, M. D., and Gelman, A. 2014. The No-U-Turn sampler: adaptively setting path lengths
- in Hamiltonian Monte Carlo. J. Mach. Learn. Res. 15: 1593-1623.
- 522 Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the
- seasonal temperature cycle. J. Fish. Res. Board Can. 34(10):1524-1550.
- 524 https://doi.org/10.1139/f77-217.
- 525 Honsey, A. E., Staples, D. F., and Venturelli, P. A. 2017. Accurate estimates of age-at-maturity
- 526 from the growth trajectories of fishes and other ectotherms. Ecol. App. 27:182-192.
- 527 https://doi.org/10.1002/eap.2017.27.issue-1.
- 528 Iles, T. D. 1974. The tactics and strategy of growth in fishes. *In* Sea fisheries research. *Edited by*
- 529 F. R. Harden Jones. Elek Science, London. pp. 331-345.
- Jensen, R. R., and Benfey, T. J. 2022. Acclimation to warmer temperature reversibly improves
- 531 high-temperature hypoxia tolerance in both diploid and triploid brook charr, *Salvelinus*
- *fontinalis*. Comp Biochem Physiol A Mol Integr Physiol 264:111099.
- 533 https://doi.org/10.1016/j.cbpa.2021.111099.
- 534 Kay, M. 2022. tidybayes: tidy data and geoms for Bayesian models. R package version 3.0.2.
- 535 Avaliable from https://cran.r-project.org/package=tidybayes.
- 536 Kearney, M. R. 2019. Reproductive hyperallometry does not challenge mechanistic growth
- 537 models. Trends Ecol. Evol. 34(4): 275-276. https://doi.org/10.1016/j.tree.2018.12.006.
- 538 Kearney, M. R. 2021. What is the status of metabolic theory one century after Pütter invented
- the von Bertalanffy growth curve? Biol. Rev. 96(2): 557-575.
- 540 https://doi.og/10.111/brv.12668.

- 541 Kitchell, J. F., Stewart, D. J., and Weininger, D. 1977. Applications of a bioenegetics model to
- 542 yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res.
- 543 Board Can. 34(10): 1922-1935. https://doi.org/10.1139/f77-258.
- 544 Kooijman, S. A. L. M. 2010. Dynamic energy budget theory for metabolic organisation.
- 545 Cambridge University Press. https://doi.org/10.1017/CBO9780511805400.
- 546 Kooijman, S. A. L. M., and Lika, K. 2014. Resource allocation to reproduction in animals. Biol.
- 547 Rev. 89(4): 849-859. https://doi.org/https://doi.org/10.1111/brv.12082.
- Lester, N. P., Shuter, B. J., and Abrams, P. A. 2004. Interpreting the von Bertalanffy model of
- somatic growth in fishes: the cost of reproduction. P. R. Soc. Lond. B. Bio. 271(1548): 1625-
- 550 1631. https://doi.org/10.1098/rspb.2004.2778.
- Lester, N. P., Shuter, B. J., Venturelli, P., and Nadeau, D. 2014. Life-history plasticity and
- sustainable exploitation: a theory of growth compensation applied to walleye management.
- 553 Ecol. Appl. 24(1): 38-54. https://doi.org/10.1890/12-2020.1.
- Lika, K., and Kooijman, S. A. L. M. 2003. Life history implications of allocation to growth versus
- reproduction in dynamic energy budgets. B. Math. Biol. 65(5): 809-834.
- 556 https://doi.org/10.1016/S0092-8240(03)00039-9.
- Long, J. M., and Grabowski, T. B. 2017. Otoliths. *In* Age and growth of fishes: principles and
- 558 techniques. Edited by M. C. Quist and D. A. Isermann. American Fisheries Society, Bethesda,
- 559 Md. pp. 189-219. https://doi.org/10.47886/9781934874486.ch9.
- 560 Marshall, D. J., and White, C. R. 2019a. Have we outgrown the existing models of growth?
- 561 Trends Ecol. Evol. 34(2): 102-111. https://doi.org/10.1016/j.tree.2018.10.005.

- 562 Marshall, D. J., and White, C. R. 2019b. Aquatic life history trajectories are shaped by selection,
- 563 not oxygen limitation. Trends Ecol. Evol. 34(3): 182-184.
- 564 https://doi.org/10.1016/j.tree.2018.12.015.
- 565 Maxime, V. 2008. The physiology of triploid fish: current knowledge and comparisons with
- 566 diploid fish. Fish Fish. 9(1): 67-78. https://doi.org/10.1111/j.1467-2979.2007.00269.x.
- 567 McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J.,
- 568 Alonso-Fernández, A., and Basilone, G. 2015. Energy acquisition and allocation to egg
- production in relation to fish reproductive strategies. Fish Fish. 16(1): 23-57.
- 570 https://doi.org/10.1111/faf.12043.
- 571 Minte-Vera, C. V., Maunder, M. N., Casselman, J. M., and Campana, S. E. 2016. Growth
- 572 functions that incorporate the cost of reproduction. Fish Res. 180: 31-44.
- 573 https://doi.org/https://doi.org/10.1016/j.fishres.2015.10.023.
- 574 Morgan, G. E. 2002. Manual of instructions fall walleye index netting (FWIN). Percid
- 575 Community Synthesis, Diagnostics and Sampling Standards Working Group, Ontario Ministry
- 576 of Natural Resources, Peterborough.
- 577 Ogle, D. H. 2019. RFishBC. R package version 0.2.3. Avaliable from https://CRAN.R-
- 578 project.org/package=RFishBC.
- 579 Ojolick, E. J., Cusack, R., Benfey, T. J., and Kerr, S. R. 1995. Survival and growth of all-female
- 580 diploid and triploid rainbow trout (*Oncorhynchus mykiss*) reared at chronic high
- 581 temperature. Aquaculture 131(3-4): 177-187. https://doi.org/10.1016/0044-8486(94)00338-
- 582 O.

- 583 Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a
- 584 generalization of von Bertalanffy's theory of growth. Ber. Deut. Wiss. Komm. 28(4): 251-282.
- Pauly, D. 2019. Female fish grow bigger let's deal with it. Trends Ecol. Evol. 34(3): 181-182.
- 586 https://doi.org/10.1016/j.tree.2018.12.007.
- Pauly, D. 2021. The gill-oxygen limitation theory (GOLT) and its critics. Sci. Adv. 7(2): eabc6050.
 https://doi.org/10.1126/sciadv.abc6050.
- 589 Piferrer, F., Beaumont, A., Falguière, J.-C., Flajšhans, M., Haffray, P., and Colombo, L. 2009.
- 590 Polyploid fish and shellfish: production, biology and applications to aquaculture for
- 591 performance improvement and genetic containment. Aquaculture 293(3-4): 125-156.
- 592 https://doi.org/10.1016/j.aquaculture.2009.04.036.
- 593 Pütter, A. 1920. Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. Pflug.
- 594 Arch. Ges. Phys. 180(1): 298-340. https://doi.org/10.1007/BF01755094.
- 595 Quince, C., Shuter, B. J., Abrams, P. A., and Lester, N. P. 2008. Biphasic growth in fish II:
- 596 empirical assessment. J. Theor. Biol. 254(2): 207-214.
- 597 https://doi.org/https://doi.org/10.1016/j.jtbi.2008.05.030.
- 598 Quist, M. C., Guy, C. S., Schultz, R. D., and Stephen, J. L. 2003. Latitudinal comparisons of
- 599 walleye growth in North America and factors influencing growth of walleyes in Kansas
- 600 reservoirs. N. Am. J. Fish. Manage. 23(3): 677-692. https://doi.org/10.1577/M02-050.
- 601 R Development Core Team. 2022. R: a language and environment for statistical computing. R
- 602 Foundation for Statistical Computing, Vienna. Available from https://www.r-project.org/.
- Rennie, M. D., Purchase, C. F., Lester, N., Collins, N. C., Shuter, B. J., and Abrams. P. A. 2008.
- Lazy males? Bioenegetic differences in energy acquisition and metabolism help explain

- sexual size dimorphism in percids. J. Anim. Ecol. 77(5): 916-926.
- 606 https://doi.org/10.111/j.1365-2656.2008.01412.x.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos, 44(2):
- 608 257-267. https://doi.org/10.2307/3544698.
- Riseth, E. N., Fraser, T. W. K., Sambraus, F., Stein, L. H., and Hvas, M. 2020. Is it advantageous
- for Atlantic salmon to be triploid at lower temperatures? J. Therm. Biol. 89: 102548.
- 611 https://doi.org/10.1016/j.jtherbio.2020.102548.
- 612 Sadoul, B., Geffroy, B., Lallement, S., and Kearney, M. 2020. Multiple working hypotheses for
- 613 hyperallometric reproduction in fishes under metabolic theory. Ecol. Model. 433: 109228.
- 614 https://doi.org/https://doi.org/10.1016/j.ecolmodel.2020.109228.
- 615 Sambraus, F., Olsen, R. E., Remen, M. Hansen, T. J., Torgersen, T., and Fjelldal, P. G. 2017. Water
- temperature and oxygen: the effect of triploid on performance and metabolism in farmed
- 617 Atlantic salmon (*Salmo salar* L.) post-smolts. Aquaculture 473: 1-12.
- 618 https://doi.org/10.1016/j.aquaculture.2017.01.024.
- Tiwary, B. K., Kirubagaran, R., and Ray, A. K. 2000. Gonadal development in triploid
- 620 *Heteropneustes fossilis*. J. Fish Biol. 57(5): 1343-1348. https://doi.org/10.1111/j.1095-
- 621 8649.2000.tb00493.x.
- Trippel, E.A., Butts, I.A.E., Babin, A., Neil, S.R.E., Feindel, N.J., and Benfey, T.J. 2014. Effects of
- reproduction on growth and survival in Atlantic cod, *Gadus morhua*, assessed by comparison
- to triploids. J. Exp. Mar. Biol. Ecol. 451: 35-43. https://doi.org/10.1016/j.jembe.2013.10.030.

- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J. B. 2000. Estimating food
- 626 consumption rates of fish using a mercury mass balance model. Can. J. Fish. Aquat. Sci. 57(2):
- 627 414-428. https://doi.org/10.1139/f99-262.
- 628 Upper Colorado River Recovery Program. 2022. Interim principles for stocking sterile walleye in
- 629 the upper Colorado River basin. Available from: https://coloradoriverrecovery.org/uc/wp-
- 630 content/uploads/sites/2/2022/06/2022_FWS_UDWR_CPW_WalleyePositionPaper_508.pdf.
- 631 Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-
- one-out cross-validation and WAIC. Stat. Comput. 27(5): 1413-1432.
- 633 https://doi.org/10.1007/s11222-016-9696-4.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II).
- 635 Hum. Biol. 10(2): 181-213.
- 636 Walker, S., P. Addison, S. Sandstrom, and N. Lester. 2013. Contact retention selectivity of three
- 637 types of gillnet gangs. Ontario Ministry of Natural Resources, Aquatic Research and
- 638 Monitoring Section, Aquatic Research Series 2013-07, Peterborough.
- 639 West, G. B., Brown, J. H., and Enquist, B. J. 2001. A general model for ontogenetic growth.
- 640 Nature, 413(6856): 628-631. https://doi.org/10.1038/35098076.
- 641 White, C. R., Alton, L. A., Bywater, C. L., Lombardi, E. J., and Marshall, D. J. 2022. Metabolic
- scaling is the product of life-history optimization. Science, 377(6608): 834-839.
- 643 https://doi.org/10.1126/science.abm7649.
- 644 White, C. R., and Marshall, D. J. 2019. Should we care if models are phenomenological or
- 645 mechanistic? Trends Ecol. Evol. 34(4): 276-278. https://doi.org/10.1016/j.tree.2019.01.006.
- 646 Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

	647	Wilson, K. L., H	lonsey, A. E., I	Moe, B.,	Venturelli, P	, and Rev	/nolds, J	J. 2017.	Growing	the bi	pha	sic
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648 framework: Techniques and recommendations for fitting emerging growth models. Methods

649 Ecol. Evol. 9(4): 822-833. https://doi.org/10.1111/2041-210x.12931.

- 650 Winemiller, K. O., and Rose, K. A. 1992. Patterns of life-history diversification in North American
- fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49(10): 2196-2218.
- 652 https://doi.org/10.1139/f92-242.
- 453 Yao, Y., Vehtari, A., Simpson, D., and Gelman, A. 2018. Using stacking to average Bayesian
- 654 predictive distributions. Bayesian Anal. 13(3): 917-1007. https://doi.org/10.1214/17-BA-
- 655 1091.
- Zohar, Y. 2021. Fish reproductive biology Reflecting on five decades of fundamental and
- translational research. Gen. Comp. Endocr. 300: 113544.
- 658 https://doi.org/10.1016/j.ygcen.2020.113544.
659 Tables

660 **Table 1.** Estimated means (μ) and standard deviations (σ) of posterior distributions for parameters of

the Pütter-von Bertalanffy growth model fit to length-at-age data for fertile and sterile walleyes.

662 Walleyes were aged using sagittal otoliths.

		Ferr	nales			Males				
	Fertile		Sterile		Fertile		Sterile			
Parameter	μ	σ	μ	σ	μ	σ	μ	σ		
L∞	592.2	5.7	579.4	14.6	493.0	2.6	472.1	6.7		
К	0.23	0.01	0.22	0.02	0.36	0.01	0.44	0.04		
t _o	-1.21	0.10	-1.15	0.29	-0.81	0.08	0.11	0.26		
σ	0.068	0.001	0.069	0.002	0.068	0.001	0.069	0.002		

663 **Notes:** L_{∞} is the asymptotic mean total length, *K* is the Brody growth coefficient, and t_0 is the

theoretical age at zero length.

Table 2. Estimated means (μ) and standard deviations (σ) of posterior distributions for parameters of the Lester biphasic growth model fit to
 length-at-age data for fertile and sterile walleyes. Walleyes were aged using sagittal otoliths. Note that the post-maturation growth phase for
 sterile walleye was removed from the LBGM as an evaluation of underlying assumptions.

	Females						Males						
	Fertile		Sterile (Phase 2)		Sterile (Phase 4)		Fe	Fertile		Sterile (Phase 2)		Sterile (Phase 4)	
Parameter	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	
L∞	592.3	13.1	-	-	534.0	17.48	495.9	3.6	-	-	477.3	10.8	
К	0.24	0.04	-	-	0.35	0.07	0.35	0.02	-	-	0.42	0.09	
t _o	-1.17	0.68	-	-	0.09	0.81	-0.75	0.27	-	-	-0.10	0.69	
Т	3.51	0.20	-	-	3.06	0.44	1.88	0.12	-	-	2.32	0.62	
t_1	174.2	5.4	252.2	4.5	198.42	49.66	121.9	4.6	271.2	5.2	-194.3	120.4	
h	68	3.1	32.4	1.0	52.38	24.11	113.7	4.7	25.6	1.1	199.7	70.2	
σ	0.067	0.001	0.082	0.002	0.07	0.005	0.067	0.001	0.082	0.002	0.07	0.005	

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Notes: L_{∞} is the asymptotic mean total length, *K* is the Brody growth coefficient, and t_1 and t_0 are parameters representing the theoretical age at

570 zero length for the juvenile portion and adult portion of the Lester biphasic growth model respectively, and *h* is the maximum growth rate.

671	Figure	Captions
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Figure 1. Hypothetical fits of the Lester biphasic growth model for (A) fertile (diploid) and (B)

sterile (triploid) walleye where h is the maximum potential growth rate, t_1 is the theoretical age

- at zero length, g is the joint energetic cost of gamete production and activity associated with
- reproduction, *T* is the age when gamete production begins, L_m is length-at-maturity, and L_{∞} is
- the average maximum size. According to the Lester biphasic growth model, sterile walleyes are
- expected to grow linearly throughout their life because they do not invest any energy into
- gamete production or reproductive activity (i.e., g = 0). Figure adapted from Wilson et al.
- 679 (2017).

Figure 2. Typical gonad development for sterile (triploid) and fertile (diploid) walleyes captured

681 immediately prior to peak spawning date. For each sex, gonads belong to fish of similar size and

age. Scale bar = 25 mm. \mathcal{P} = Female, σ = Male.

Figure 3. Observed length- and age-frequecny histograms for fertile (diploid) and sterile

684 (triploid) walleye. Median ages from multiple otolith readings were used for plotting observed

age-frequency data. F = Female, M = Male.

Figure 4. Growth model fits to observed length-at-age data for fertile (diploid) and sterile

- 687 (triploid) walleye. Solid lines show mean predicted total length for fertile walleye, and dot-
- dashed lines for sterile walleye. Ribbons show 95% credible intervals. Median ages from
- 689 multiple otolith readings were used for plotting observed data.
- 690 **Figure 5.** Standardized residual plots vs. age for fertile (diploid) and sterile (triploid) walleye
- 691 from fits of the Lester biphasic (LBGM) and Pütter-von Bertalanffy (P-VBGM) growth models.

Sex-specific colored lines were fit with a LOESS Local Quadratic Regression with a spanning parameter of 0.75. Deviation from the dotted line at zero indicates a lack of fit. **Figure 6.** Sex-specific posterior probabilities that sterile walleyes are longer (TL = total length [mm]) than fertile walleyes for males (M) and females (F) using 1,000 draws from the posterior fits of the P-VBGM from age-0 to age-14 (bin size = 0.1 years). *T* is the age when allocation of energy to gonads begins for fertile walleyes as estimated by logistic maturity-at-age-regression (T_M = 1.88 years, T_F = 3.51 years).

699 **Figure 7.** Posterior distributions of L_{∞} , the mean asymptotic total length (mm), estimated by the 700 Pütter-von Bertalanffy Growth Model.

Figure 8. Posterior distributions of *T*, the age at which allocation of energy to reproduction
 begins, one year prior to age-at-50% maturity (Lester et al. 2004). Posterior distributions of *T* for fertile fish were estimated with a logistic regression using age-at-maturity data. Posterior
 distributions of *T* for sterile fish were estimated by fitting the full Lester Biphasic Growth Model

to age-at-length data.

Figure 9. Daily averaged surface and bottom water temperatures in Narraguinnep Reservoir

from 2019-2021 measured with Onset HOBO Pendant UA-002-08 temperature loggers. The

optimal water temperature for consumption (CTO, dashed line) for walleye is 22°C, and the

709 maximum water temperature above which consumption ceases (CTM, dot-dashed line) for

710 walleye is 27°C (Kitchell et al. 2017; Deslauriers et al. 2017).

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Figure 1. Hypothetical fits of the Lester biphasic growth model for (A) fertile (diploid) and (B) 714 715 sterile (triploid) walleye where h is the maximum potential growth rate, t_1 is the theoretical age at zero length, g is the joint energetic cost of gamete production and activity associated with 716 717 reproduction, T is the age when gamete production begins, L_m is length-at-maturity, and L_{∞} is 718 the average maximum size. According to the Lester biphasic growth model, sterile walleyes are expected to grow linearly throughout their life because they do not invest any energy into 719 720 gamete production or reproductive activity (i.e., g = 0). Figure adapted from Wilson et al. 721 (2017).



- **Figure 2.** Typical gonad development for sterile (triploid) and fertile (diploid) walleyes captured
- immediately prior to peak spawning date. For each sex, gonads belong to fish of similar size and
- age. Scale bar = 25 mm. = Female, σ = Male.



727 **Figure 3.** Observed length- and age-frequecny histograms for fertile (diploid) and sterile

- 728 (triploid) walleye. Median ages from multiple otolith readings were used for plotting observed
- 729 age-frequency data. F = Female, M = Male.

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Figure 4. Growth model fits to observed length-at-age data for fertile (diploid) and sterile
(triploid) walleye. Solid lines show mean predicted total length for fertile walleye, and dotdashed lines for sterile walleye. Ribbons show 95% credible intervals. Median ages from
multiple otolith readings were used for plotting observed data.







Figure 6. Sex-specific posterior probabilities that sterile walleyes are longer (TL = total length742[mm]) than fertile walleyes for males (M) and females (F) using 1,000 draws from the posterior743fits of the P-VBGM from age-0 to age-14 (bin size = 0.1 years). *T* is the age when allocation of744energy to gonads begins for fertile walleyes as estimated by logistic maturity-at-age-regression745(T_M = 1.88 years, T_F = 3.51 years).



Figure 7. Posterior distributions of L_{∞} , the mean asymptotic total length (mm), estimated by the





Figure 8. Posterior distributions of *T*, the age at which allocation of energy to reproduction
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Figure 9. Daily averaged surface and bottom water temperatures in Narraguinnep Reservoir
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maximum water temperature above which consumption ceases (CTM, dot-dashed line) for
walleye is 27°C (Kitchell et al. 2017; Deslauriers et al. 2017).

<u>RESEARCH PRIORITY</u>:

Walleye oxytetracycline marking: Exploring the potential of mass marking Walleye with oxytetracycline.

OBJECTIVES

The primary objective of this priority was to determine if oxytetracycline (OTC) could be used effectively to mark Walleye from multiple water sources.

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 (*Sander vitreus*) 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).

An OTC marking protocol was applied and evaluated that was developed by Brooks et al. (1994) and refined by the Minnesota Department of Natural Resources (see Logsdon et al. 2004). 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 treatment. This procedure was attempted several times within Colorado and met with varying degrees of success. Initial collaborations with Colorado State University using their equipment for detecting OTC marks were unsuccessful (Lepak 2013). Multiple fish species and hard structures were prepared and analyzed, but no marks were detected.

At first, ineffective marking/detection was assumed to be related to the chemical makeup of the water being used for marking. During consultation with personnel at Minnesota Department of Natural Resources, it was clear that source water alkalinity and oxygen were important factors influencing the success of OTC marking. The importance of maintaining adequate oxygen levels during marking is obvious for survival. However, using source water with the correct alkalinity is more complex. When emersion water alkalinity is elevated (>60 mEq/L; Minnesota Department of Natural Resources, pers. comm.), it requires less buffer to increase the emersion solution to the desired pH of 6.8. This is important because an excess of buffer (> 1:1 buffer to OTC) will precipitate OTC out of solution, leaving little for fish uptake. Waters in Colorado tend to be relatively low in alkalinity, thus, we caution that source water alkalinity should be quantified and exceed 60 mEq/L prior to any marking efforts.

Despite the initial failure to detect OTC marks on fish hard structures, further efforts using two ultraviolet lamps with no other light sources enabled researchers to detect OTC marks externally and on most hard structures. The lamps were manufactured by Ultra-violet Products Incorporated located in San Gabriel, California, and equipped with 100-watt Sylvania mercury spotlight bulbs. This method facilitated the detection of OTC marks, but without the ability to effectively use a microscope, the application was limited (Lepak 2013). However, given the success with the ultraviolet lamps, there was confidence that fish had been marked successfully using the technique described by Brooks et al. (1994) and refined by the Minnesota Department of Natural Resources (see Logsdon et al. 2004).

These observations prompted further investigation and consultation with Minnesota and Nebraska personnel to determine the best methodology and equipment for detecting OTC marks. Additional efforts to detect OTC marks were made with fish that had been marked under the best conditions possible (using relatively high alkalinity water from the Bellvue Hatchery, Bellvue, CO). We selected a subset of 18 Walleye (9 treated with OTC and 9 controls) from an OTC marking event in 2012. During this effort Walleye were transported to the CPW Fort Collins Service Center, Fort Collins, CO. Fish were placed in two coolers (treatments and control) with 30 L of well water from the Bellvue Hatchery. An aeration stone was placed in each cooler to ensure adequate levels of dissolved oxygen. A silicon-based surfactant (ProLine® defoamer) was added to each cooler at a concentration of 0.013 mL/L to prevent foaming. These fish were held for several months under different light conditions to evaluate external OTC mark retention. The 9 treated Walleye were mortalities from the dark experimental treatments.

We were fortunate to collaborate on this project with Jeff Schuckman and Brad Newcomb from Nebraska Game and Parks through a connection with Ken Kehmeier (CPW). We prepared walleye otoliths using mounting techniques (super glue directly on glass slides) recommended by these collaborators (Lepak 2014). These otoliths were transported to Nebraska Game and Parks where they were evaluated using their Nikon Eclipse 55i microscope with an Exfo X-Cite 100W UV light source with a BA-S151F barrier filter and a 510 nm diachronic mirror. Of the 18

walleye otoliths prepared and inspected from the experimental design described above, there was 100% agreement between four readers (2 trained and 2 untrained) about whether or not otoliths were from marked individuals. There was one exception to this where two readers categorized the otolith as being marked, while the other two were unable to classify the otolith as marked or not marked, and all four readers said the otolith needed slightly more preparation. The otolith was polished briefly and all four readers agreed it was from a marked individual, which it was (Lepak 2014). These results were promising, and the magnified image at the right shows an example of the yellow coloration versus the green background of a marked otolith.



Initial image of an OTC-marked Walleye fingerling otolith. This Walleye was marked by Colorado Parks and Wildlife and the image was taken with Nebraska Game and Parks equipment. The mark is yellow on the green background.

PROJECT PROGRESS

These findings from a decade ago confirmed that under the right conditions (Bellvue, CO water source) we could successfully mark Walleye fingerlings and detect the marks on otoliths months later with microscopy. The results also prompted the acquisition of an in-house microscope and light/filter combination to detect OTC marks on otoliths (Olympus trinocular microscope equipped with an Incident Fluorescence Attachment with Blue Excitation Cube, 100W HBO Housing and HBO103 Lamp and assorted filters). However, the concern remained that mass-marking Walleye using water from the Pueblo Hatchery (Pueblo, CO) may not be possible due to water conditions and potential precipitation inhibiting OTC uptake. To assess this concern in spring 2024 Walleye were marked with water from multiple sources and OTC mark detections from otoliths were compared across sources and to control, unmarked Walleye. On 28 May 2024 Walleye from the Pueblo Hatchery were marked using the modified Brooks et al. (1994) OTC marking method refined by Logsdon et al. (2004) with water from the Bellvue Hatchery, the Pueblo Hatchery, and Pueblo Reservoir. These fish were transported from the Pueblo Hatchery



during marking and held in Fort Collins in aerated 75-200 L flow through tanks. Walleye tanks were cleaned as needed (generally daily), and Walleye were fed *Daphnia* and blood worms to encourage growth. On 10 June 2024, 9 Walleye from each water source were collected and their otoliths were extracted and mounted on glass slides with super glue. There were also 9 fingerling Walleye available from 2022 that were raised in the Pueblo Hatchery and collected before stocking at Chatfield Reservoir (Denver, CO).

RESULTS & DISCUSSION

We confirmed external marks on live Walleye in May with ultraviolet lamps, and on otoliths from mortalities during the experiment (28 October 2024). All interpreters (n = 4) were able to identify marked otoliths (n = 27) from Walleye with 100% accuracy, and no control (n = 9) otoliths were classified as marked. These findings were confirmed on both otoliths when available (n = 70 of 72 possible).

Walleye otoliths marked with OTC were compared to control Walleye that were unmarked. Water from the Bellvue Hatchery was used for fish marked in column 1, while water from the Pueblo Hatchery was used for control (column 2) and marked fish (column 3), and Pueblo Reservoir was used for marked fish in column 4. Yellow/orange rings are clearly visible on marked Walleye otoliths (column 1, 3, and 4).

REFERENCES

Brooks, R. C., R. C. Heidinger, and C. C. Kohler. 1994. Mass-marking otoliths of larval and juvenile walleye by immersion in oxytetracycline, calcein, or calcein blue. North American Journal of Fisheries Management. 14:143-150.

Lepak, J. M. 2013. Annual Lake and Reservoir Research Report. Colorado Parks and Wildlife. Annual Report, Fort Collins, CO, USA.

Lepak, J. M. 2014. Annual Lake and Reservoir Research Report. Colorado Parks and Wildlife. Annual Report, Fort Collins, CO, USA.

Logsdon, D. E., B. J. Pittman, and G. C. Barnard. 2004. Oxytetracycline marking of newly hatched walleye fry. North American Journal of Fisheries Management. 24:1071-1077.

RESEARCH COMMUNICATION & TECHNICAL ASSISTANCE

Reporting period: December 2023 – November 2024.

Peer-Reviewed Publications

- Beauchamp, D. A., A. G. Hansen, and D. Parrish. 2024. Chapter 7: Coldwater fish in large standing waters. *In* Standard methods for sampling North American freshwater fishes (2nd edition). *Edited by* S.A. Bonar, W.A. Hubert, and D.W. Willis. American Fisheries Society, Bethesda, Maryland.
- Farrell, C. J., A. G. Hansen, M. M. Brandt, C. M. Myrick, and B. M. Johnson. 2024. An evaluation of the relative size, body condition, and survival of triploid walleye in the wild. *North American Journal of Fisheries Management* 44:172–188.
- Lepak, J. M., W. M. Pate, P. Cadmus, A. G. Hansen, K. D. Gallaher, and D. B. Silver. 2024. Response of an invasive aquatic crustacean to the fish toxicant rotenone. Lake and Reservoir Management. 40(3):330-337.
- Hansen, A. G., J. M. Lepak, E. I. Gardunio, and T. Eyre. 2024. Evaluating harvest incentives for suppressing a socially-valued, but ecologically-detrimental, invasive fish predator. Fisheries Management and Ecology 31:e12699.
- 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. *In press*. Cyclical, multi-trophic-level responses to a volatile, introduced forage fish: learning from four decades of food web observation to inform management. Fisheries.
- Shiqi Li, Chao Guo, Chuansong Liao, Jie Ke, A. G. Hansen, Xuefeng Shi, Jiashou Liu, Tanglin Zhang, E. Jeppesen, and Wei Li. 2024. Improvement of water quality through coordinated multi-trophic level biomanipulations: application to a subtropical emergency water supply lake. Science of the Total Environment 955:176888.

Manuscripts Submitted for Publication

- Chao Guo, Wei Li, A. G. Hansen, Shiqi Li, Jie Ke, Chuansong Liao, Jing Yuan, Chuanbo Guo, Jiashou Liu. *Submitted*. Diverse foraging in small-bodied fishes: effects on water quality and submerged macrophytes in shallow subtropical lake ecosystems. Environment International.
- Chao Guo, Wei Li, Shiqi Li, Chuansong Liao, Jie Ke, Xingwei Chi, A. G. Hansen, Chuanbo Guo, and Jiashou Liu. *In revision*. Density-dependent effects of zooplanktivorous thin sharpbelly (*Toxabramis swinhonis*) on plankton communities and water quality: implications for lake restoration. Water Biology and Security.

- Hansen, A. G., J. M. Lepak, W. M. Pate, D. Brauch, and B. W. Avila. *Submitted*. Not just water over the dam: upstream ecosystem disruption following reoperation for environmental flows. Ecological Applications.
- Farrell, C. J., B. M. Johnson, A. G. Hansen, B. W. Avila, and C. A. Myrick. *In revision*. Induced sterility illuminates the effects of reproduction on growth. Canadian Journal of Fisheries and Aquatic Sciences.

Manuscripts in Preparation

• Walsworth, T. E., A. G. Hansen, and J. M. Lepak. Life-stage dependent impacts of prey species drive cyclic dynamics of a top predator population. Submitting to Canadian Journal of Fisheries and Aquatic Sciences.

External Presentations

- Lepak, J. M. Manipulation of sport fish growth to reduce mercury bioaccumulation on a whole-system scale. Guest lecture for Dr. Rozanne Razavi. Syracuse University. Feb. 2024 (virtual).
- Walsworth, T. E., A. G. Hansen, and J. M. Lepak. Untangling drivers of cyclic walleye dynamics. 2024 Utah Chapter of the American Fisheries Society. Feb. 2024.
- Lepak, J. M. Characterizing lake and reservoir ecosystems: simple and complex models. Invited Lecture: Front Range Community College. Fort Collins, CO. Apr. 2024.
- Beauchamp, D. A., A. G. Hansen (primary presenter), and D. Parrish. Chapter 7: Coldwater fish in large standing waters. Annual National American Fisheries Society Meeting, Honolulu, HI. Sept. 2024 (oral presentation).
- Beauchamp, D. A., A. G. Hansen (primary presenter), and D. Parrish. Chapter 7: Coldwater fish in large standing waters. Annual National American Fisheries Society Meeting, Honolulu, HI. Sept. 2024 (poster presentation).

Internal Presentations

- Lepak, J. M. Tiger Muskellunge update, College Lake comparison, Grand Lake mesocosms. CPW Coldwater Reservoir Meeting. Virtual. Feb. 2024.
- Lepak, J. M. Lake and Reservoir Research Projects. CPW Aquatic Section Meeting. Feb. 2024.
- Hansen, A. G. Lake and Reservoir Research Projects. CPW Aquatic Section Meeting. Feb. 2024.

- Brandt, M., A. G. Hansen, and J. M. Lepak. Converting to the North American Standard: Evaluation of CPW vs. AFS Gill Nets. CPW Aquatic Biologist Summit. Feb. 2024.
- Brandt, M., A. G. Hansen, and J. M. Lepak. Converting to the North American Standard: Evaluation of CPW vs. AFS Gill Nets. CPW Northeast Biodays. Apr. 2024.

Other Research Communication & Technical Assistance

- Anonymous peer reviewer for: Fishes (3), Biology (1), North American Journal of Fisheries Management (2), Aquaculture, Fish and Fisheries (1), Canadian Journal of Fisheries and Aquatic Sciences (1), Hydrobiologia (1), Fish and Fisheries (1), Fisheries Research (1), and FACETS (1).
- Provided analytical assistance to Mandi Brandt regarding CPW versus AFS gill netting comparisons.
- Provided expertise on species- and system-specific sport fish mercury bioaccumulation for the Technical Advisory Committee for fish consumption advice in Colorado led by CDPHE personnel (Meghan Williams and Aki Suzuki).
- Consultations on tiger muskellunge stocking with Carrie Tucker (Trinidad), Dan Brauch (Lake San Cristobal), Jon Ewert (Shadow Mountain), Tory Eyre (Elkhead Reservoir), and Kristina Morben (reciprocal cross, interactions with northern pike, and holdover information), Eric Gardunio (multiple systems), Estevan Vigil (Sanchez Reservoir).
- Consultation with Eric Gardunio regarding triploid walleye monitoring in Ridgway Reservoir.
- Consultation with Quentin Springer at Pueblo Hatchery regarding triploid walleye production.
- Provided assistance confirming the age (32 years) of Bighead Carp in Tomlinson Park Pond with Aubrey Pelletier.
- Consultation about thiamine, thiaminase and docosahexaenoic acid (Kevin Rogers).