Lake and Reservoir Research

Adam G. Hansen, Ph.D.
Aquatic Research Scientist

Jesse M. Lepak, Ph.D.
Aquatic Research Scientist

William M. Pate
Colorado State University

Collin J. Farrell
Colorado State University

Annual Report

Colorado Parks & Wildlife
Aquatic Research Section
317 West Prospect Road
Fort Collins, Colorado

December 2023

STATE OF COLORADO

Jared Polis, Governor

COLORADO DEPARTMENT OF NATURAL RESOURCES

Dan Gibbs, Executive Director

COLORADO PARKS & WILDLIFE

Jeff Davis, Director

WILDLIFE COMMISSION

AQUATIC RESEARCH STAFF

George J. Schisler, Aquatic Research Leader
Kelly Carlson, Aquatic Research Program Assistant
Pete Cadmus, Aquatic Research Scientist/Toxicologist, Water Pollution Studies
Tawni Riepe, Aquatic Research Scientist/Toxicologist, Water Pollution Studies
Eric R. Fetherman, Aquatic Research Scientist, Salmonid Disease Studies
Ryan Fitzpatrick, Aquatic Research Scientist, Eastern Plains Native Fishes
Eric E. Richer, Aquatic Research Scientist/Hydrologist, Stream Habitat Restoration
Matthew C. Kondratieff, Aquatic Research Scientist, Stream Habitat Restoration
Dan Kowalski, Aquatic Research Scientist, Stream and River Ecology
Adam G. Hansen, Aquatic Research Scientist, Coldwater Lakes and Reservoirs
Jesse M. Lepak, Aquatic Research Scientist, Cool and Warmwater Lakes and Reservoirs
Zachary Hooley-Underwood, Aquatic Research Scientist, Western Slope Native Fishes
Kevin B. Rogers, Aquatic Research Scientist, Cutthroat Trout Studies
Andrew J. Treble, Aquatic Research Scientist, Aquatic Data Management and Analysis
Brad Neuschwanger, Hatchery Manager, Fish Research Hatchery
Tracy Davis, Hatchery Technician, Fish Research Hatchery
Troy Meyer, Hatchery Technician, Fish Research Hatchery

Karen Hertel, Librarian

Prepared by:____
Adam G. Hansen, Aquatic Research Scientist

Jesse Lepak

Prepared by:____
Jesse M. Lepak, Aquatic Research Scientist

Approved by:____
George J. Schisler, Aquatic Wildlife Research Chief

Date:_____12/4/23_______________

TABLE OF CONTENTS

LAKE AND RESERVOIR RESEARCH

Period covered: December 2022 – November 2023.

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

Response to rotenone by *Mysis diluviana*: LC50 concentrations exceed application recommendations

Jesse M. Lepak[a*], William M. Pate[a], Pete Cadmus[a], Adam G. Hansen[a], Kiah D. Gallaher[a]

[a] Colorado Parks and Wildlife, 317 West Prospect Rd. Fort Collins, CO 80526

[*] Corresponding author: Email: jesse.lepak@state.co.us, Phone: 970-657-5820

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).

Keywords: Aquatic invertebrates, *Daphnia*, Invasive species control, Kokanee salmon, *Mysis relicta*, Zooplankton

Introduction

Fisheries managers have used the application of the piscicide rotenone for decades in aquatic systems to control or eradicate fish species for a variety of purposes including non-native species control and native fish conservation and restoration efforts [1-3]. Although widely used because of selective toxicity to fish and some invertebrates [4], the effects of rotenone (e.g., sublethal or other effects on non-target species like invertebrates) are not fully understood, and study continues to understand potential unintended impacts [5,6]. Generally, Ephemeropterans, Plecopterans, and Trichopterans are sensitive to rotenone relative to other aquatic invertebrates [7-9], while zooplankton have been found to be even more sensitive than groups of larger macroinvertebrates [5,10]. However, invertebrates generally have tolerances to rotenone that exceed the tolerances of fish by order(s) of magnitude, so application concentration targets are generally thought of in terms of their impacts on fish species [5,11].

Throughout Scandinavia and northern North America *Mysis diluviana* (opossum shrimp; formerly known as *M. relicta*) have been introduced primarily to improve foraging opportunities for sport fish. These introductions were done largely because of a single successful example in 1949 from Kootenay Lake in British Columbia [12,13]. In Kootenay Lake, *M. diluviana* introduction resulted in a significant increase in kokanee salmon (*Oncorhynchus nerka*) growth, but this was an anomaly [14]. Instead, widespread introductions proved unsuccessful, creating competitive conditions between introduced *M. diluviana* and salmon and trout for cladocerans and other food resources [13,15]. Further, *M. diluviana* migrate daily, foraging near the surface at night, but residing in deeper sediments during the day, making them relatively unavailable to visual feeders like salmon and trout [16]. In general, it was concluded that most salmon and trout fisheries throughout northwestern North America were negatively impacted by *M. diluviana* introductions [17]. Due to these interactions, eradication of *M. diluviana* has been considered appealing by managers where introductions have resulted in established *M. diluviana* populations that reduce cladoceran densities and subsequently salmonid growth [18].

Control of *M. diluviana* using rotenone is appealing because of decades of research and documentation of responses by aquatic life to rotenone applications. However, there is reason to believe that the use of rotenone to control *M. diluviana* may not be effective at ecologically feasible concentrations because of some of their characteristics. For example, *M. diluviana* breath through their carapace (not tracheal gills) and are relatively large compared to some other invertebrates commonly evaluated (e.g., *Daphnia spp*), though they do spend much of their time at the water-sediment interface, making them more vulnerable to treatment [5,6,19]. However, the combination of these factors and their influence on the efficacy of rotenone applications to eradicate/control *M. diluviana* have not been tested previously on freshwater *Mysids*. Here we evaluate the 50% lethal concentrations (LC50s) for *M. diluviana* at 24, 48, 96, and 192-hours using rotenone concentrations within, and exceeding recommended application limits (0 to 90 mg/L) to determine the efficacy of rotenone as a control measure.

Methods

On 11 May 2016, *M. diluviana* were collected from Carter Reservoir (Larimer County, CO, USA) at night using a 1 m diameter net (1 mm mesh) towed horizontally. Handling of *M. diluviana* and study design were informed using USEPA guidelines [20,21]. Individuals were transported in lake water to a water bath in the laboratory and held in reconstituted water (matching Carter Reservoir water following ASTM 2023 guidelines [22] at approximately 10 °C ($CaSO_4$= 30 mg/L, KCl = 2 mg/L, $MgSO_4$= 30 mg/L, and $NaHCO_3$ = 48 Mg/L). A laboratory culture of *Daphnia spp* was used to feed *M. diluviana* daily *ad libitum* until treatments were initiated on 17 and 23 May 2016, respectively. Prior to, and during trials, *M. diluviana* were held under dark conditions. When light was necessary for transfer and assessments of mortality, only red light was used to diminish any effects on *M. diluviana* from light sensitivity. Trials beginning on 17 May were used to establish feasible and relevant treatment and testing conditions. Following these trials, concentrations of 0, 1, 2, 4, 10, 30, and 90 mg/L Legumine CFT (5% active rotenone for target concentrations of 0, 50, 100, 200, 500, 1,500 and 4,500 ppb) were selected for evaluation. Rotenone concentrations were determined using high performance liquid chromatography (HPLC; P. Cadmus has additional details), and realized mean empirical concentrations for treatments were 0.4, 46.0, 83.0, 160.0, 384.5, 1472.5, and 3248.4 ppb (Table 1).

Table 1. Target and measured rotenone concentrations.

Active rotenone (target ppb)	Mean empirical rotenone (ppb)	Variance (ppb)	Range (ppb)	n
0	0.4	0.1	0-2	4
50	46.0	1.1	43-48	4
100	83.0	1.6	76-92	10
200	160.0	8.9	137-178	4

500	384.5	NA	384-385	2
1500	1472.5	512.9	564-2791	4
4500	3248.4	415.0	1364-4134	7

Target and mean concentrations are provided followed by the variance and range of measured rotenone concentrations (ppb) and the sample size (n) for each corresponding set of targets/measurements.

After a 12-day holding/acclimation period under laboratory conditions, *M. diluviana* were transferred into acid washed and triple rinsed glass jars with 800 mL of reconstituted water (described above). A renewal approach was taken during the trials where every 24-hours jars were siphoned down to 200 mL and refilled to 800 mL (repeated four times) with water matching in previous chemistry and rotenone concentration. Trials consisted of six replicate control jars and four replicate jars of every rotenone concentration tested. Each jar began with eight randomly assigned individual *M. diluviana*. Trials were conducted at approximately 8 °C, relatively cold for toxicity trials, but a relevant temperature for *M. diluviana*. Mortalities were evaluated (and removed) at 24-hour intervals, and LC50s were determined at 24, 48, 96 and 192-hours. Median LC50s and their 95% confidence intervals (CI) were estimated by fitting two-parameter log-logistic functions to observed mortality responses across rotenone concentrations using the dose-response curve (drc) package [23] in R [24].

Results

At 24 and 48-hours, no rotenone concentration tested resulted in > 25% mortality of *M. diluviana* and fitted log-logistic functions failed to converge within drc. Significant dose-response curves were observed at 96 and 192-hours. The fitted model for each exposure duration passed the lack-of-fit test ($p \geq 0.26$). For the 96 and 192-hour exposures, only the highest concentrations of rotenone tested resulted in mortality approaching or exceeding 50% (Fig 1). In addition, the estimated median LC50s exceeded concentrations (200 ppb active rotenone) and commonly evaluated exposure times recommended/allowable for treatment on the landscape. The estimated 96-hour LC50 was 9,989.4 (SE = 3,118.6; 95% CI = 3,601.2-16,377.6) ppb rotenone, and 606.5 (125.3; 349.8-863.2) ppb rotenone at 192-hours. The estimated 96-hour LC50 exceeded recommended application limits of rotenone by ~50-fold.

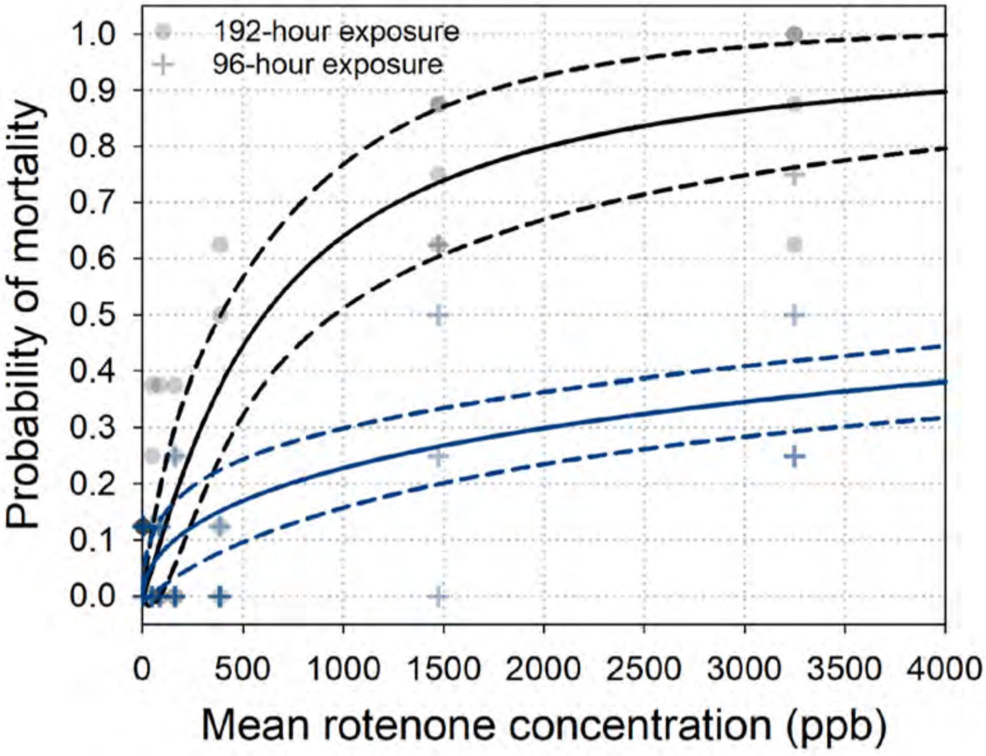

Fig 1. Rotenone dose-responses of *M. diluviana*. Estimated probabilities of mortality (solid lines) for *M. diluviana* at 96 and 192-hours are provided as a function of rotenone concentration (ppb). Points are observed data and overlapping points have corresponding darker shading. Each treatment began 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.

Discussion

These results represent the first toxicity test of rotenone on *M. diluviana* of which we are aware, and results indicate that rotenone is likely not a viable control method. Sublethal effects and population-level impacts have been observed in invertebrate communities in response to rotenone treatments, but when compared to most fish species *ceteris paribus*, impacts appear to be relatively minimal or short-lived [e.g., 7,8,25]. In the case of *M. diluviana*, rotenone concentrations and exposure times required to reach 50% lethality exceed application recommendations like many other invertebrates, and would be detrimental to other aquatic species (like most fish) more vulnerable to rotenone [5,11]. This rotenone tolerance is likely due to *M. diluviana* characteristics including the lack of tracheal gills and their relatively large size compared to some other sensitive aquatic fauna [5,6,19]. To our knowledge, only one other mysid (*Praunus flexuosus*, a marine species) has an established LC50 for rotenone in the literature (27 h at 250 ppb active rotenone in ~10 °C water), which was a lower tolerance than what we observed for *M. diluviana* under our experimental conditions [26]. Notably, mortality approaching 50% is not ideal when management objectives are focused on the control or eradication of organisms (versus establishing protective thresholds).

Having control methods available for *M. diluviana* is still desirable for managers. Major components of lake and reservoir food webs can be comprised of *M. diluviana*, reaching densities over 1,000 m^2 in some cases in their native range and systems where they have been introduced [27,28]. Indeed there are examples of what were considered positive impacts on fisheries from *M. diluviana* introductions like increasing growth rates of trout and salmon in

Kootenay Lake, and reservoir tailwater fisheries where *M. diluviana* are entrained and provide forage for fish downstream [14,29,30]. However, these circumstances were unique, and negative, unintended consequences are prevalent in conjunction with *M. diluviana* introductions. Arguably the most important detrimental food web perturbation to native and sport fish connected with *M. diluviana* introductions is alteration of the zooplankton community [12,31]. For example, in Flathead (Montana, USA) and Pend Oreille (Idaho, USA) lakes *M. diluviana* introductions were connected to the decline/collapse of cladoceran communities and subsequently kokanee salmon [32-35]. Thus, measures for controlling *M. diluviana* populations remain appealing for managers focused on maintaining and/or enhancing sport fisheries, particularly salmonids like kokanee salmon that rely heavily on zooplankton as a food resource.

Although controlling *M. diluviana* populations may be appealing to managers, relatively few options have become apparent. Perhaps some of the most promising suggestions for controlling introduced and established *M. diluviana* populations have been related to biological control (Martinez and Bergersen 1989). There are some instances where *M. diluviana* densities have declined concomitant with biological introductions. For example, in Lake Champlain (New York and Vermont, USA) the *M. diluviana* population declined by ten-fold in conjunction with an invasion by dreissenid mussels [36], and the authors hypothesized that this decline resulted from the establishment of dreissenid mussels and was sustained by the presence of alewife (*Alosa pseudoharengus*) and rainbow smelt. Many systems in Colorado (USA) have been exposed to *M. diluviana* through stocking in the 1950's to the 1970's, and established populations appear to have persisted [28] where lake morphometry (primarily depth and size) is considered suitable, with one exception. In Horsetooth Reservoir (Colorado, USA), rainbow smelt were introduced in 1983, and during periods when they achieve relatively high densities, *M. diluviana* (introduced in the early 1970's) become absent during routine surveys [37]. Alternatively, when the rainbow smelt population declined significantly in Horsetooth Reservoir, *M. diluviana* were observed again during sampling efforts [37], suggesting that biological control may be feasible in some cases.

Conclusion

Although rotenone treatments represent a potential method for controlling invasive *M. diluviana* populations, the exposure times/concentrations required for effective control appear to be at levels where other fauna would be negatively impacted. Thus, rotenone efforts focused on *M. diluviana* are likely to be in conflict with fisheries objectives to support native and sport fish growth and abundance. For example, control efforts using rotenone intended to benefit cladocerans and subsequently salmonids by reducing competition for forage would likely result in mortality (and other sublethal effects) in cladocerans and salmonids before impacting the target *M. diluviana* population. In the context of *M. diluviana* control, our results suggest rotenone treatment likely represents an inadequate option under most conditions in which control strategies would be considered desirable. Future work should focus on other compounds for evaluation, identifying additional biological control options, or control methods that take advantage of other potential vulnerabilities of *M. diluviana* like sensitivity to light and warm temperatures.

Acknowledgements

We thank the numerous employees, faculty, and staff from Colorado Parks and Wildlife and Colorado State University that have contributed to what is known about *M. diluviana*. We thank Patrick Martinez in particular for leading a variety of efforts focused on *M. diluviana* research in Colorado. We also thank Ben Galloway for assisting with laboratory experiments.

References

[1] McClay W. Rotenone use in North America (1988-1997). Fisheries. 2000;20: 15-21. doi: 10.1577/1548-8446(2000)025%3C0015:RUINA%3E2.0.CO;2

[2] McClay W. Rotenone use in North America (1998-2002). Fisheries. 2005;30: 29-31. doi: 10.1577/1548-8446(2005)30[29:RUINA]2.0.CO;2

[3] Finlayson B, Schnick R, Skaar D, Anderson J, Demong L, Duffield D, Horton W, Steinkjer J. Planning and standard operating procedures for the use of rotenone in fish management – rotenone SOP manual, 2nd edition. Bethesda: American Fisheries Society. 2018 [cited 2023 Nov 15]: [176 p]. Available from: https://units.fisheries.org/rotenone-stewardship/sop-manual/rotenone-sop-manual-2nd

[4] Fukami J, Shishido T, Fukunaga K, Casida JE. Oxidative metabolism of rotenone in mammals, fish, and insects and its relation to selective toxicity. J Agr Food Chem. 1969;17(6): 1217-1226. doi: 10.1021/jf60166a048

[5] Vinson MR, Dinger EC, Vinson DK. Piscicides and invertebrates: after 70 years, does anyone really know? Fisheries. 2010;35(2): 61-71.

[6] Kjærstad G. The eradication of invasive species using rotenone and its impact on freshwater macroinvertebrates. Ph.D. dissertation, Norwegian University of Science and Technology. 2022. Available from: https://ntnuopen.ntnu.no/ntnu-xmlui/handle/11250/2988431?locale-attribute=en

[7] Mangum MA, Madrigal JL. Rotenone effects on aquatic macroinvertebrates of the Strawberry River, Utah: a five-year summary. J Freshwater Ecol. 1999;14: 125-135. doi: 10.1080/02705060.1999.9663661

[8] Eriksen TE, Arnekleiv JV, Kjærstad G. Short-term effects on riverine ephemeroptera, plecoptera, and trichoptera of rotenone and aluminum sulfate treatment to eradicate *Gyrodactylus salaris*. J Freshwater Ecol. 2009;24: 597-607. doi: 10.1080/02705060.2009.9664337-edition/

[9] Hamilton BT, Moore SE, Williams TB, Darby N, Vinson MR. Comparative effects of rotenone and antimycin on macroinvertebrate diversity in two streams in Great Basin National Park, Nevada. N Am J Fish Manage. 2009;29: 1620- 1635. doi: 10.1577/M08-178.1

[10] Beaulieu J, Trépanier-Leroux D, Fischer JM, Olson MH, Thibodeau S, Humphries S, Fraser DJ, Derry AM. Rotenone for exotic trout eradication: nontarget impacts on aquatic communities in a mountain lake. Lake Reserv Manage. 2021;37: 323-338. doi: 10.1080/10402381.2021.1912864

[11] Ling N. Rotenone—a review of its toxicity for fisheries management. New Zealand Department of Conservation, Science for Conservation 211. 2002 [cited 2023 Nov 15]: [40 p]. Available from: https://www.doc.govt.nz/documents/science-and-technical/sfc211.pdf

[12] Northcote TG. Success, problems, and control of introduced mysid populations in lakes and reservoirs. In: Nesler TP, Bergersen EP, editors. Mysids in fisheries: hard lessons from headlong introductions. Bethesda: American Fisheries Society Symposium. 1991;9: 5-16.

[13] Lasenby DC, Northcote TG, Fürst MF. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Can J Fish Aquat Sci. 1986;43: 1277-1284.

[14] Sparrow RAH, Larkin PA, Rutherglen RA. Successful introduction of *Mysis relicta* Lovén into Kootenay Lake, British Columbia. J Fish Res Board Can. 1964;21: 1325-1327.

[15] Martinez PJ, Bergersen EP. 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: American Fisheries Society Symposium. 1991;9: 49-64.

[16] Beeton AM, Bowers JA. Vertical migration of *Mysis relicta* Lovén. Hydrobiologia. 1982;93: 53-61.

[17] Nesler TP, Bergersen EP. Mysids in fisheries: hard lessons from headlong introductions. Bethesda: American Fisheries Society Symposium. 1991. 199 pp.

[18] Martinez PJ, Bergersen EP. Proposed biological management of *Mysis relicta* in Colorado lakes and reservoirs. N Am J Fish Manage. 1989;9: 1-11.

[19] Rudstam LG, Melnik NG, Shubenkov SG. Invertebrate predators in pelagic food webs: Similarities between *Macrohectopus branickii* (Crustacea: Amphipoda) in Lake Baikal and *Mysis relicta* (Crustacea: Mysidaceae) in Lake Ontario. Siberian Journal of Ecology. 1998;5: 429-434.

[20] USEPA (United States Environmental Protection Agency). Ecological effects test guidelines OPPTS 850.1035 mysid acute toxicity test. Washington, DC: EPA 712–C–96–136. 1996 [cited 2023 Nov 15]: [10 p]. Available from: https://nepis.epa.gov/Exe/ZyPDF.cgi/P100G6R3.PDF?Dockey=P100G6R3.PDF

[21] USEPA (United States Environmental Protection Agency). Methods for measuring the acute toxicity of effluents and receiving waters to freshwater and marine organisms, fifth edition.

Washington, DC: EPA-821-R-02-012. 2010 [cited 2023 Nov 15]: [275 p]. Available from: https://www.epa.gov/sites/default/files/2015-08/documents/acute-freshwater-and-marine-wet-manual_2002.pdf

[22] ASTM International. Standard guide for conducting acute toxicity tests on test materials with fishes, macroinvertebrates, and amphibians. Guide E729-23e1. 2002 [revised 2023 Feb 22; cited 2023 Nov 15]: [23 p.]. Available from: https://dx.doi.org/10.1520/E0729-23E01 doi: 10.1520/E0729-23E01

[23] Ritz C, Baty F, Streibig JC, Gerhard D. Dose-response analysis using R. PLoS ONE. 2015;10(12): e0146021. doi: 10.1371/journal.pone.0146021

[24] R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. 2011.

[25] Covi JA, Hutchison ER, Neumeyer CH, Gunderson MD. Rotenone decreases hatching success in brine shrimp embryos by blocking development: implications for zooplankton egg banks. PLoS ONE. 2016;11(9): e0163231. doi: 10.1371/journal.pone.0163231

[26] Næss T, Naas KE, Samuelsen OB. Toxicity of rotenone to some potential predators on marine fish larvae - an experimental study. Aquacult Eng. 1991;10(3): 149-159.

[27] Jude DJ, Rudstam LG, Holda TJ, Watkins JM, Euclide PT, Balcer MD. Trends in *Mysis diluviana* abundance in the Great Lakes, 2006–2016. J Great Lakes Res. 2018;44: 590-599.

[28] Silver DB, Johnson BM, Pate WM, Hansen AG, Christianson KR. History and outcomes of Opossum Shrimp (*Mysis diluviana*) introductions in Colorado. Fort Collins: Colorado Parks and Wildlife Technical Publication 58. 2021 [cited 2023 Nov 15]: [348 p]. Available from: https://cpw.state.co.us/Documents/Research/Aquatic/pdf/Publications/2021-Opossum-Shrimp-History-Outcomes.pdf

[29] Griest JR. The lake trout of Twin Lakes, Colorado. REC-ERC-77-4. 1977 [cited 2023 Nov 15]: [39 p]. Available from: https://www.usbr.gov/tsc/techreferences/rec/REC-ERC-77-04.pdf

[30] Nehring RB. Effects of reservoir escapement of mysids on two Colorado tailrace trout fisheries. In: Nesler TP, Bergersen EP, editors. Mysids in fisheries: hard lessons from headlong introductions. Bethesda: American Fisheries Society Symposium. 1991;9: 134-143.

[31] Beattie WD, Clancey PT. Effects of *Mysis relicta* on the zooplankton community and kokanee population of Flathead Lake, Montana. In: Nesler TP, Bergersen EP, editors. Mysids in fisheries: hard lessons from headlong introductions. Bethesda: American Fisheries Society Symposium. 1991;9: 39-48.

[32] Rieman BE, Falter CM. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. T Am Fish Soc. 1981;110: 613-620. doi: 10.1577/1548-8659(1981)110<613:EOTEOM>2.0.CO;2

[33] Ellis BK, Stanford JA, Goodman D, Stafford CP, Gustafson DL, Beauchamp DA, Chess DW, Craft JA, Deleray MA, Hansen BS. Long-term effects of a trophic cascade in a large lake ecosystem. P Natl Acad Sci-Biol. 2011;108(3): 1070-1075. doi: 10.1073/pnas.1013006108

[34] Devlin SP, Tappenbeck SK, Craft JA, Tappenbeck TH, Chess DW, Whited DC, Ellis BK, Stanford JA. Spatial and temporal dynamics of invasive freshwater shrimp (*Mysis diluviana*): long-term effects on ecosystem properties in a large oligotrophic lake. Ecosystems. 2017;20, 183-197. doi: 10.1007/s10021-016-0023-x

[35] Corsi MP, Hansen MJ, Quist MC, Schill DJ, Dux, AM. Influences of lake trout (*Salvelinus namaycush*) and *Mysis diluviana* on kokanee (*Oncorhynchus nerka*) in Lake Pend Oreille, Idaho. Hydrobiologia. 2019;840: 351-362. doi:10.1007/s10750-019-3889-8

[36] Ball SC, Mihuc TB, Myers LW, Stockwell JD. Ten-fold decline in *Mysis diluviana* in Lake Champlain between 1975 and 2012. J Great Lakes Res. 2015;41: 502-509. doi: 10.1016/j.jglr.2015.03.002

[37] Hansen AG. Coldwater lake and reservoir research projects. Fort Collins: Colorado Parks and Wildlife. 2021 [cited 2023 Nov 15]: [152 p]. Available from: https://www.researchgate.net/publication/358622829_Coldwater_Lake_and_Reservoir_Research_Projects_2021_Annual_Report_Colorado_Parks_and_Wildlife

RESEARCH PRIORITY: **Summer Profundal Index Netting (SPIN) for monitoring Lake Trout *Salvelinus namaycush*:** Results from 2023 sampling on Ruedi Reservoir.

OBJECTIVES

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

INTRODUCTION

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

Summer Profundal Index Netting (SPIN) is a quantitative survey method for rapidly estimating the density of Lake Trout (Sandstrom and Lester 2009). Previous investigations by Colorado Parks and Wildlife concluded that SPIN is a viable alternative to more intensive methods for estimating and tracking trends in the abundance of Lake Trout to help guide management (Lepak 2011; Lepak 2013). Four water bodies have been sampled using SPIN: Taylor Park Reservoir (surveyed in 2013), Lake Granby (2014), Grand Lake (2013, 2016), and Blue Mesa Reservoir (2011, 2014, 2016, 2018, and 2020-2022). Results from the 2023 survey on Ruedi 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 two days from August 23-24, 2023 wherein 30 nets were set, capturing a total of 106 Lake Trout ranging in size from 209 mm to 999 mm total length (TL; mean = 378 mm ± 104 mm SD). However, 92% of Lake Trout encountered ranged between 275 and 450 mm TL. Lake Trout were most prevalent in 20-30 m depths. The depth distribution, size structure, and extent of the catch in 2023 at the corresponding water surface elevation of Ruedi Reservoir produced a total Lake Trout abundance estimate of 10,050 fish ≥209 mm TL (lower 68% confidence limit = 8,443; upper limit = 11,913). The catch of Lake Trout <275 mm TL was incidental (2.8%). Therefore, this abundance estimate best reflects fish ≥275 mm TL (Table 1). Compared to other reservoirs sampled, Ruedi Reservoir, which contains invasive *Mysis diluviana*, exhibited a relatively high density of Lake Trout (Table 1).

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

Survey year	Lake or reservoir	Number of net sets	Number of Lake Trout caught	Mean total length (mm)	SD of total length (mm)	Adjusted CUE	Density (fish/ha)	Total area surveyed (ha)	Abundance estimate	LCL	UCL
2011											
	Blue Mesa	81	129	437	110	2.29	11.14	3,059	34,071	27,144	41,929
2013											
	Grand Lake*	36	87	419	107	2.61	12.71	193	2,452	1,974	2,996
	Taylor Park*	36	271	416	94	4.03	19.61	610	11,950	9,871	14,341
2014											
	Blue Mesa	81	211	425	97	1.61	7.85	3,409	26,753	18,383	33,716
	Lake Granby*	71	501	417	79	11.78	57.26	2,780	159,193	135,533	186,844
2016											
	Blue Mesa	83	180	438	114	1.47	7.15	3,409	24,368	16,538	30,948
	Grand Lake*	36	109	436	147	3.34	16.22	193	3,131	2,561	3,783
2018											
	Blue Mesa	95	313	414	98	2.34	11.36	2,629	29,857	23,826	36,702
2020											
	Blue Mesa	90	212	441	92	1.51	7.32	2,247	16,443	12,518	20,842
2021											
	Blue Mesa	90	121	465	126	1.23	5.97	1,637	9,775	7,213	12,627
2022											
	Blue Mesa	79	151	364	106	1.45	7.06	1,768	12,477	9,451	15,864
2023											
	Ruedi*	30	106	378	104	6.36	30.90	325	10,050	8,443	11,913

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: Calibrating Fall Walleye Index Netting (FWIN) for application in Colorado.

OBJECTIVES

Evaluate the appropriateness of FWIN for assessing adult Walleye *Sander vitreus* in key Colorado reservoirs and develop Colorado-specific estimates of gill net catchability that enable conversion of catch per unit effort to density.

PUBLICATION

Hansen, A. G., M. W. Miller, E. T. Cristan, C.J. Farrell, P. Winkle, M.M. Brandt, K.D. Battige, and **J. M. Lepak**. 2023. Gill net catchability of Walleye (*Sander vitreus*): Are provincial standards suitable for estimating adult density outside the region? Fisheries Research 266:106800.

BACKGROUND

Multi-mesh gill nets are commonly used for the assessment of freshwater fish populations given their ease of deployment and ability to provide an index of relative abundance (i.e., catch per unit effort [CPUE]) that can be compared through time when following standard protocols (Bonar et al. 2017). Although gill net CPUE is considered appropriate for routine monitoring, direct estimates of abundance facilitate more comprehensive assessments, such as identifying sustainable harvest strategies (e.g., Lenker et al. 2016) or characterizing predator-prey interactions (e.g., Pate et al. 2014), often required for informing management decisions. However, estimating abundance directly typically requires mark-recapture methods, which can be cost and resource prohibitive. Understanding the relationship between gill net CPUE and fish abundance (i.e., catchability of the gear) would broaden the applicability of standard protocols, and permit use of analytical approaches better suited for time series of absolute rather than relative abundance (Gutowsky et al. 2019; Giacomini et al. 2020). Walleye are an important sport and food fish in Colorado. Examining and calibrating established sampling protocols such as FWIN could provide a useful tool for when more in-depth assessments are needed for addressing management questions.

MANUSCRIPT ABSTRACT

Standard gill netting protocols are increasingly used to assess freshwater fish populations. Understanding the catchability (q) of fish following these protocols enables direct estimation of density, which has advantages over relative abundance from analytical and applied research perspectives. However, catchability is complex. The application of q estimated in one region may be inappropriate for another if physical and biological processes driving catchability differ. Cross-region assessments of q are needed to assess the applicability of estimates over a broader geographic and environmental range. In this study, we evaluated whether the global estimate of q (1.044 ha/gang; variance = 0.2268) derived by Giacomini et al. (2020) for Walleye 350 mm total length (TL) was suitable for application in two Colorado, USA reservoirs supporting recreational fisheries and wild spawn operations. We followed provincial standards in Ontario and Quebec,

Canada (i.e., Fall Walleye Index Netting) combined with other corrections for size-dependent catchability to estimate the density of mature, adult Walleye ≥470 mm TL for comparison to independent estimates from mark-recapture analyses. Following similar methodologies, we found that the global estimate of *q* combined with size-dependent gill net retention coefficients underestimated the density of adults by nearly 80%, but uncertainty in point estimates can be high. Results highlighted the need to better understand sources of uncertainty, including factors influencing size-dependence in gill net encounter when extending estimates of *q* to other size classes of fish, systems, and regions. Estimates of catchability for large-bodied adult Walleye in our systems were consistent, but relatively low, ranging from 0.203 ha/gang (95% confidence limits = 0.133–0.298) to 0.227 ha/gang (0.091–0.556). We expand the geographic and environmental range of paired mark-recapture and gill net catch per unit effort information and discuss potential factors contributing variability to estimates of catchability for adult Walleye.

REFERENCES

Bonar, S. A., N. Mercado-Silva, W. A. Hubert, T. D. Beard Jr., G. Dave, J. Kubecka, B. D. S. Graeb, N. P. Lester, M. Porath, and I. J. Winfield. 2017. Standard methods for sampling freshwater fishes: opportunities for international collaboration. Fisheries 42:150–156.

Giacomini, H. C., N. P. Lester, P. Addison, S. Sandstrom, D. Nadeau, C. Chu, and D. T. de Kerckhove. 2020. Gillnet catchability of Walleye (*Sander vitreus*): comparison of North American and provincial standards. Fisheries Research 224:105433.

Gutowsky, L. F., H. C. Giacomini, D. T. de Kerckhove, R. Mackereth, D., McCormick, and C., Chu. 2019. Quantifying multiple pressure interactions affecting populations of a recreationally and commercially important freshwater fish. Global Change Biology 25:1049–1062.

Lenker, M. A., B. C. Weidel, O. P. Jensen, and C. T. Solomon. 2016. Developing recreational harvest regulations for an unexploited Lake Trout population. North American Journal of Fisheries Management 36:385–397.

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.

RESEARCH PRIORITY: **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 SUBMISSION

Hansen, A. G., **J. M. Lepak**, E. I. Gardunio, and T. Eyre. *In review*. Controlling socially-valued, but ecologically-detrimental fish: evaluating harvest incentives for suppressing an invasive predator. Fisheries Management and Ecology.

FULL MANUSCRIPT

Controlling socially-valued, but ecologically-detrimental fish: evaluating harvest incentives for suppressing an invasive predator

Adam G. Hansen[1*], Jesse M. Lepak[1], Eric I. Gardunio[2], and Tory Eyre[3]

[1]Colorado Parks and Wildlife, Aquatic Research Section, Fort Collins, Colorado, USA

[2]Colorado Parks and Wildlife, Montrose, Colorado, USA

[3]Colorado Parks and Wildlife, Meeker, Colorado, USA

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 salmoides*) 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 was temporally-variable within the same system, suggesting opportunity to adapt tournament structure 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.

KEYWORDS

Angling, control programs, invasive species, native biodiversity, removal, smallmouth bass

INTRODUCTION

Anthropogenic modifications, especially the assisted migration of aquatic invasive species, threaten freshwater biodiversity and ecosystems worldwide (Dungeon et al., 2006; Strayer & Dungeon, 2010). Many invaders have been introduced because they are perceived as valuable in some way(s) to humans (Simberloff et al., 2013). This includes many fishes, which have had a complex history of introductions driven by shifting social-ecological values. For example, during the early settlement of the United States, intentional fish introductions were common with the goal of providing sustenance or recreational opportunity. Unfettered introductions were later viewed as harmful to native biota and ecosystems as the fields of ecology and conservation developed, leading to the enactment of regulations that restricted further spread and implementation of control programs (Rahel & Smith, 2018). However, historic introductions combined with continued natural or unauthorized dispersal has homogenized fish faunas and fostered social tensions over the control of long-valued, but simultaneously ecologically-detrimental species (Rahel, 2000; Johnson et al., 2009).

Control efforts are important for mitigating the impacts of invasive fishes (Zipkin et al., 2009; Pearson et al., 2022), but can be opposed if counter to public opinions or perceptions (Gozlan et al., 2013). Further, control of invasive species can be challenging, costly, and unceasing unless eradication is achieved (Holmes et al., 2015). Overcoming these obstacles may require unconventional control strategies as part of a more integrated solution to the management of invasive, yet socially-valued species (Dunham et al., 2020). Relatively small-scale eradications have been apparently successful (Koenig et al., 2015; Simberloff, 2021; Tiberti et al., 2021), and it is suggested that eradication of some invasive fish (e.g., sea lamprey, *Petromyzontidae marinus*) is theoretically possible at scales as large as the U.S. Great Lakes when applying conventional control methods concomitant with new techniques like gene drive (Adams et al., 2021; Jones & Adams, 2021). In practice, however, eradication is difficult to achieve, and most control programs have seen variable success (Rytwinski et al., 2019; Simberloff, 2021). In addition, even if eradication is ecologically feasible or successful, the continual prospect of re-invasion from adjacent localities in open systems (Pearson et al., 2019), or new unauthorized introductions into closed systems, could undermine previous control efforts (Dunham et al., 2020). The latter concern is particularly relevant to the control of socially-valued invasive fishes given their history of unauthorized spread. This dynamic emphasizes the need for control programs that incorporate rather than exclude public stakeholders, and facilitate outreach and education to help shift social perceptions to be more inclusive of native biodiversity (Johnson et al., 2009; Rahel & Smith, 2018).

One particularly charismatic and widely spread invasive fish species is smallmouth bass (*Micrpoterus dolomieu*). Smallmouth bass are among the most sought-after freshwater sport fish species in North America (United States Census Bureau, 2016). However, nonnative smallmouth bass are now one of the most commonly addressed species in the invasive fish control/mitigation literature (Rytwinski et al., 2019). Smallmouth bass are problematic because of their ability to exert high levels of predation on native fishes (Vander Zanden et al., 1999; Weidel et al., 2000; Vander Zanden et al., 2004; Warner, 2005; Johnson et al., 2008). In addition, smallmouth bass are highly fecund and have large reproductive potential, which is a common characteristic of successful and difficult to control invaders across a diversity of taxa (Costantino et al., 1997; Pardini et al., 2009; Zipkin et al., 2009; Duron et al., 2017). Smallmouth bass continue to spread through assisted or natural dispersal in western North America (e.g., Kirk et al., 2022) and elsewhere (e.g., South Africa; Khosa et al., 2019). As a result, smallmouth bass have been the target of multiple control programs to benefit native species in both lotic and lentic ecosystems (Weidel et al., 2007; Hawkins et al., 2009).

The social-ecological tradeoffs associated with invasive smallmouth bass control make them a model species for testing unconventional or largely dismissed mitigation strategies. First, conflict with recreational anglers can arise if control programs do not incorporate them or consider their culture and ethics. For example, the growing contingent of sport anglers for invasive smallmouth bass in Washington State, USA are against sacrificing individuals, so mandatory harvest is not viable (Aday et al., 2009; Carey et al., 2011). Similarly, liberalizing harvest has been dismissed as a viable control strategy (Boucher, 2005; Gomez & Wilkinson, 2008; Loppnow et al., 2013). Unconventional approaches are needed to harmonize tensions between conservation and recreational goals in this context (Mueller, 2005; Cowx et al., 2010).

One approach is to offer cash- or prize-based harvest incentives. Incentives have boosted angler participation and played integral roles in some large-scale predator control efforts, but are usually implemented in tandem with other independent removal methods that exclude anglers (e.g., Dux et al., 2019). Further, paying anglers on a per fish basis in addition to the cost of other supplementary management or implementation efforts can be prohibitive, so cost-effective alternatives are needed.

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 (Simberloff, 2009). 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, USA. To address this objective, we quantified the harvest dynamics of anglers during a series of incentive-based fishing tournaments on each reservoir. The tournaments occurred in June or July and varied in duration (9 days versus 24 days). As a result, we could estimate angler participation and effectiveness and corresponding harvest rates under alternative conditions and tournament structures. We used field data collected at the onset of each control program to parameterize an age-structured model and simulate the dynamics of smallmouth bass. The model was used to explore potential short- and long-term responses to continuous annual harvest pressure, and to identify avenues for increasing control program efficacy.

METHODS

Study region and reservoirs

The Colorado River basin contains critical habitat for the endemic Colorado pikeminnow (*Ptychocheilus lucius*), humpback chub (*Gila cypha*), bonytail chub (*Gila elegans*), and razorback sucker (*Xyrauchen texanus*). However, the basin is heavily impounded with several reservoirs representing sources of nonnative predators like northern pike (*Esox lucius*) and smallmouth bass that have dispersed and established populations that threaten native fishes in riverine habitats downstream (Johnson et al., 2009; Wolff et al., 2012). For example, smallmouth bass were recently (July 2022) found in the lower Colorado River from Lake Mead due to extended drought conditions facilitating entrainment, and could threaten reaches considered strong-holds for native fishes such as humpback chub (Healy et al., 2020).

Reservoirs for this study are located in the upper Colorado River basin. Elkhead is a mesotrophic 364 ha impoundment (maximum depth = 17.7 m) at 1,927 m elevation on Elkhead Creek, a tributary to the Yampa River in northwestern Colorado. The reservoir thermally stratifies during the summer and surface temperatures reach 18-22°C. The fishery is managed for largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), and bluegill sunfish (*Lepomis macrochirus*), which are all considered compatible with downstream conservation efforts (Martinez et al., 1994). Smallmouth bass introductions were authorized (agency stocked in 1978), but the reservoir is a known source population to critical habitat in the Yampa River (Breton et al., 2013). To limit escapement, a net spanning the spillway was installed in 2016. In addition, incentivized harvest was initiated in 2016.

Ridgway is an oligotrophic 392 ha impoundment (maximum depth = 61.0 m) at 2,094 m elevation on the Uncompahgre River in southwestern Colorado, upstream of critical habitat in the lower Gunnison River. The reservoir thermally stratifies by late June, and surface temperatures reach 18-22°C. The fishery is managed for naturally reproducing brown trout (*Salmo trutta*) and stocked rainbow trout (*Oncorhynchus mykiss*), but non-native white sucker (*Catostomus commersonii*), stocked kokanee (*O. nerka*), and unauthorized yellow perch (*Perca flavescens*) are present. The introduction of smallmouth bass was also unauthorized and they were first confirmed in the reservoir in 2013, but anglers reported their presence 5 years prior. Similar to Elkhead, a rigid fish screen was constructed around the spillway in 2022 to limit escapement, but incentivized smallmouth bass harvest started earlier (2015).

Harvest tournaments and incentive structures

In Elkhead, we measured fish population and angler responses during fishing tournaments from 24 June to 2 July 2017, 23 June to 1 July 2018, and 22-30 June 2019. Timing and duration of tournaments was constant across years and used a raffle-based incentive structure, supplemented with one “prize” smallmouth bass tagged internally using a Passive Integrated Transponder (PIT; 12 mm Biomark or HDX from Oregon RFID) that was undetectable by anglers. Individual anglers received one raffle ticket for each smallmouth bass caught (independent of size) and turned into the on-sight PIT scanning/fish measurement station staffed daily by agency personnel. If the PIT tagged fish was caught, the angler received a cash award (check) of $1,500 USD. If the PIT tagged fish was not caught, the check was awarded via raffle drawing. A $750 USD check was issued to the angler who caught and turned in the most smallmouth bass cumulatively across the tournament. Additional physical prizes (e.g., fishing gear) were awarded daily throughout the tournament for the smallest, largest, and most smallmouth bass caught (totaling $2,250 USD).

In Ridgway, tournaments ran from 11-19 June 2015, 4-12 June 2016, and 7-30 July 2017. The 2017 tournament was moved to July and extended to assess for potential differences in the catchability of smallmouth bass. The tournaments used a raffle-based structure and PIT tagged smallmouth bass (ten annually) to award prizes with the exception of 2017 (described below). One "grand prize" (Guide V-14 Tracker boat and trailer with 5-hp Mercury outboard; $4,500 USD), and ten secondary physical prize packages each valuing $300 USD, were used as incentives. Of the ten PIT tagged fish, one was randomly selected as the grand prize winner and announced at the end of the tournament. An angler won the grand prize if they turned in the smallmouth bass with the winning PIT tag. Anglers won secondary prize packages for the other PIT tagged smallmouth bass in the order that they were turned in. If no, or not all PIT tags were returned, a raffle at the conclusion of the tournament determined winners. In 2017, prize giveaways were entirely raffle-based and smallmouth bass were not PIT tagged.

Pre-tournament data collection

In each reservoir, smallmouth bass were sampled using boat electrofishing within a 2-week period prior to each tournament to characterize population size-structure and to tag fish for mark-recapture analyses. Either the entire perimeter, or predominate habitats occupied by smallmouth bass in every region of the reservoir, were targeted to maximize the number of marked fish. A single Smith-Root 5.0 GPP unit (Smith-Rout, Inc., Vancouver, WA, USA) was used in Ridgway, while two or three ETS units (ETS Electrofishing Systems, LLC, Madison, WI, USA) were used in Elkhead. Captured fish were sexed (if possible), weighed (wet weight in g; WW), measured (TL in mm), and marked with a year-specific fin clip. All smallmouth bass encountered independent of size were marked, except during 2015 on Ridgway, when only fish ≥150 mm TL were marked. On multiple occasions within each year on each reservoir, a subsample of tagged individuals (~30 fish) were held in nearshore net-pens overnight to assess short-term handling/tagging mortality. No mortality was observed. To the extent possible, fish were released in the same general region in which they were captured.

Tournament data collection

In both reservoirs, fish caught by each angler were measured for TL, inspected for a mark and PIT tag, and counted at a central-check station. At first check-in, each licensed angler provided contact information and received an individual identification number. Total effort (sum of hours fished since previous check-in) it took for each angler to obtain the submitted catch was recorded to estimate catch·hour^{-1} and quantify cumulative "effective" (i.e., hours leading to the capture of at least one smallmouth bass by an angler) tournament effort. Anglers were given the option to donate their catch for research (except during the first year of each tournament). In all tournaments the majority of smallmouth bass (≥90%) were donated. These fish were placed on ice and later frozen at -20°C until they could be processed for biological samples in the laboratory.

Biological samples

We extracted and sectioned left sagittal otoliths (*n* = 795 for Elkhead and 637 for Ridgway across years) from systematic random subsamples (10-15 fish per 25 mm size-bin) taken from donated smallmouth bass for age and growth analysis. We also evaluated the maturity status of all male (*n* = 648 and 1,192) and female (*n* = 730 and 1,530) smallmouth bass donated each year.

Otoliths were aged independently by two experienced readers. After aging was complete, readers convened to reach consensus on disagreeing age assignments.

Growth was expressed using a von Bertalanffy growth function (vBGF) fit to mean length-at-age data combined across years using maximum likelihood estimation in R 3.3.2 (R Development Core Team, 2021):

$$L_a = L_\infty \cdot (1 - e^{-K \cdot (a - t0)}), (1)$$

where L_a is mean TL at age a, L_∞ is the asymptotic average TL, K is a growth rate coefficient, and $t0$ is the hypothetical age at which a fish has zero length (Quinn & Deriso, 1999). A single model instead of separate models was sufficient to describe length-at-age for both sexes in each reservoir, so data were combined. Next, we estimated the length-dependent probability of maturity of male and female smallmouth bass (P_{male} and P_{female}) using logistic regression fit to the binary response data (combined across years) in R:

$$P_{male} \ or \ P_{female} = \frac{e^{(\beta_0 + \beta_1 \cdot \mathrm{TL})}}{1 + e^{(\beta_0 + \beta_1 \cdot \mathrm{TL})}}, (2)$$

where β_0 and β_1 are fitted parameters for each sex (Table 1). Logistic regression models (Figure 1b) and the fitted vBGFs (Figure 1a) were used to estimate sex- and age-dependent probabilities of maturity for the population model.

Abundance and age-structure

Year-specific (t) starting numbers-at-age ($N_{a,t}$) were specified as inputs to the population model for both reservoirs (Table 1; Figure 1c,d). First, we estimated the annual pre-tournament abundance ($\widehat{N}$) of smallmouth bass using Chapman's estimator (Seber, 1982; Hayes et al., 2007):

$$\widehat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1, (3)$$

where n_1 = the number marked from boat electrofishing, n_2 = the number captured by anglers during the tournament, and m_2 = the number of marked fish captured by anglers. Variance was approximated as:

$$V(\widehat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} - 1, (4)$$

and 95% confidence intervals ($\alpha = 0.05$; $Z_{\alpha/2} = 1.96$) as:

$$\widehat{N} \pm Z_{\alpha/2}\sqrt{V(\widehat{N})}. (5)$$

We partitioned $\widehat{N}$ into 25 mm length bins based on the year-specific length-frequency of fish sampled boat electrofishing. Numbers-at-age were estimated by applying age-frequencies to abundance estimates partitioned by length that were tabulated from system-specific age-length-keys using age data combined across years (Ricker, 1975; Isely & Grabowski, 2007). We explored correcting length-frequency distributions for the size-dependent capture efficiency of boat electrofishing (Beamesderfer & Rieman, 1988; Bayley & Austin, 2002). However, these corrections resulted in an apparent underrepresentation of larger fish, based on the known number removed. Therefore, we assumed the uncorrected catch was representative of the population vulnerable to anglers.

Mark-recapture estimates were computed for two size-classes of smallmouth bass prior to partitioning abundance into different length bins and applying system-specific age-length-keys to minimize bias associated with differences observed in the size-selectivity of boat electrofishing (used to mark fish) versus angling (used to recapture fish; Ricker, 1975). Abundance was estimated for fish 75-149 mm TL separately from fish ≥150 mm TL (considered adults and largely ≥age-3) when smallmouth bass were fully recruited to both sampling gears and females began maturing (Table 2).

Harvest, exploitation, and catchability

Year-specific (t) harvest-at-age ($h_{a,t}$) was estimated by applying system-specific age-length-keys to the number and length-frequency of smallmouth bass caught by anglers. In both systems, age-specific exploitation rates ($\mu_{a,t}$) were calculated by dividing $h_{a,t}$ by $N_{a,t}$. We then linked effort to exploitation rate using a catchability coefficient ($q_{a,t}$; proportion of an age-class harvested after one unit [1,000 hours] of effective fishing effort). Catchability-at-age was estimated as:

$$q_{a,t} = h_{a,t} / E_t \cdot N_{a,t}, \text{ (6)}$$

where E_t is the total cumulative effective effort in hours from the fishing tournament in year t. We characterized catchability-at-age with a double logistic function fit using maximum likelihood estimation assuming a normal error structure in R:

$$q_{a,t} = \frac{1}{1 + e^{-b_2(a-b_1)}} \times \left(1 - \frac{1}{1 + e^{-b_4(a-b_3)}}\right), \text{ (7)}$$

where b_1 to b_4 are fitted parameters for each reservoir-month combination (Table 1; Figure 1e).

Catchability can vary inversely with abundance (Peterman & Steer, 1981; Shuter et al., 1998). Whether a similar relationship exists for smallmouth bass has not been evaluated, but could have important implications for a harvest-based control program. We used a 58-year time series of catchability and abundance data derived for smallmouth bass most vulnerable to catch and harvest by anglers (those ≥age-5) in Lake Opeongo, Ontario, Canada (Shuter et al., 1987) to develop an empirical relationship ($R^2 = 0.73$) for this species:

$$q_{opeongo} = 0.507e^{-0.000248 \cdot Nvuln}, \text{ (8)}$$

where N_{vuln} is the number of smallmouth bass vulnerable to anglers in the population (Figure 1f). Data were adjusted for temporal changes in creel survey effectiveness and nature of the fishery (harvest vs. catch and release) over the study period following the methods of Shuter et al. (1987) prior to fitting the exponential relationship. Because N_{vuln} is represented by fish ≥age-3, not ≥age-5 in our study systems, we used the empirical relationship from Lake Opeongo to generate scaling factors for adjusting our estimates of catchability-at-age based on age-3+ abundance (Figure 1f).

Natural survival rate

We used catch curve regression for smallmouth bass age-3 and older (fully recruited and comprised descending limbs) sampled with boat electrofishing during the second year of tournaments on each reservoir (2017 in Elkhead and 2016 in Ridgway) to estimate their annual survival rate in the absence of fishing mortality (S). Computations were based on relationships among total instantaneous mortality rate (Z), total annual mortality rate (A, where $A = 1 - e^{-Z}$), the observed exploitation rate (μ) of fish age-3 and older during the first tournament year on each reservoir (2016 and 2015 for Elkhead and Ridgway, respectively), and the expectation of natural death (v, where $v = A - \mu$). From here, $S = 1 - v$ (Miranda & Bettoli, 2007; Slipke & Maceina, 2013). Because adult abundance was not estimated on Elkhead during the first tournament, we approximated μ based on the total adult smallmouth bass removed in 2016 and the pre-tournament abundance of adults observed in 2017 (Table 1).

Recruitment

The number of age-1 recruits entering the population the year following the fishing tournaments ($N_{1,t+1}$) was calculated as a function of the number of mature male and female spawners ($N_{s,t}$) present using the Ricker stock-recruitment model (Zipkin et al., 2008):

$$N_{1,t+1} = \alpha N_{s,t} \cdot (e^{-\beta N_{s,t}}) \cdot e^{\varepsilon}. \quad (9)$$

The parameter α represents the maximum number of recruits per spawner, β governs density dependence, and e^{ε} ($\varepsilon \sim N[\mu = 0, \sigma > 0]$) created random lognormal deviates around the underlying deterministic relationship. We approximated α and β by assuming the smallmouth bass populations in Elkhead and Ridgway were at an intermediate spawning stock size where density-dependent recruitment is near its peak ($N_s = 1/\beta$ and $N_1 = \alpha/\beta e$ at peak; Ricker, 1975; Hansen et al., 2010). We first estimated β based on the number of male and female spawners (N_s) present in 2017 for Elkhead ($\beta = 1/3{,}119$) and 2015 for Ridgway ($\beta = 1/2{,}392$). To estimate α, we used the number of age-1 recruits in 2018 for Elkhead ($N_1 = 3{,}721$) and 2016 for Ridgway ($N_1 = 2{,}119$) back-calculated based on natural survival from the number of age-2 fish present in 2019 for Elkhead ($N_{2,2019} = 2{,}634$) and 2017 for Ridgway ($N_{2,2017} = 1{,}553$) derived via mark-recapture (Table 1; Figure 1g,h). Lastly, we estimated σ (i.e., recruitment variation) based on interannual variation in the boat electrofishing catch rates of age-1 smallmouth bass during spring marking surveys (Table 1).

Simulation model

We developed a stochastic age-structured population model to simulate the short- and long-term dynamics of adult smallmouth bass ≥age-3 (reflective of the predominant spawning stocks) under the most contemporary tournament design and observed effort level in each reservoir (9 days in late June for Elkhead and 24 days in July for Ridgway). Stochasticity was incorporated by including random normal error (year-by-year) into the process of natural survival and observed fishing effort, and lognormal error into the process of recruitment (Table 1). The model tracked numbers-at-age over consecutive years and followed a sequence reflective of a type I fishery whereby the populations were first subject to a non-continuous period of fishing mortality from the tournaments ($q_{a,t} \cdot E_t$ term) and survivors were then subject to natural mortality (S_t):

$$N_{a+1,t+1} = (1 - q_{a,t} \cdot E_t) \cdot N_{a,t} \cdot S_t, \ for\ 1 < a < n, \ (10)$$

where $q_{a,t}$ is month and reservoir specific (Figure 1e), and n was set to a maximum age of 18 (Beamesderfer & North, 1995). The number of age-1 recruits in year $t+1$ was computed using equation (11) and the corresponding number of male and female spawners was calculated as:

$$N_{s,t} = \sum_{a=1}^{n} \left(N_{a,t} \cdot Prop_m \cdot P_{male,a}\right) + \sum_{a=1}^{n} \left(N_{a,t} \cdot Prop_f \cdot P_{female,a}\right), \ (11)$$

which assumed spawning occurred prior to the tournaments and where $Prop_m$ and $Prop_f$ represent the proportion male versus female, respectively (Table 1).

Short-term dynamics were evaluated by simulating the model 1,000 times with each projection extending for 30 years. We assumed catchability-at-age was either fixed through time independent of abundance, or varied inversely with abundance (Figure 1f). We computed the mean abundance trajectory of smallmouth bass ≥age-3 and calculated the corresponding percent change in mean abundance at simulation year 10, 20, and 30. We summarized the distribution of simulated values using the lower 16th and upper 84th percentiles (reflecting a 68% confidence interval; CI) and the lower 2.5th and upper 97.5th percentiles (reflecting a 95% CI) of simulated values in each year. Stochasticity was removed and simulations were extended until abundance and age-structure stabilized to estimate equilibrium conditions. We estimated equilibrium abundances across fishing efforts and corresponding adult harvest rates to identify average, threshold values required for achieving long-term unsustainability (i.e., where equilibrium abundance dropped below 2 fish). Lastly, we conducted a local sensitivity analysis by manipulating each model parameter governing vital rates (growth, maturity, survival, and recruitment) by ±10% and computing percent changes in abundance at year 30 and threshold effort levels and adult harvest rates required for achieving long-term unsustainability. We assumed catchability was fixed through time and observed effort levels when evaluating parameter sensitivity.

RESULTS

Smallmouth bass demographics and angler dynamics

The smallmouth bass population in each reservoir exhibited similar growth patterns (Figure 1a) and size- and sex-dependent maturity schedules (Figure 1b), though, smallmouth bass in Elkhead exhibited slightly greater mean sizes-at-age until approximately age-8 (Figure 1a). The estimated abundances (and densities) of adult smallmouth bass (≥150 mm TL) were similar between reservoirs, ranging from 2,286 (±95% CI = 533) to 3,907 (787) in Elkhead and 3,501 (433) to 3,758 (751) in Ridgway (Table 2). However, the age-structure of each population differed, and more age-classes were detected in Elkhead (up to age-16) than in Ridgway (up to age-12; Table 1). Yet, both populations were dominated by smallmouth bass younger than age-6 by the third year of tournaments when model simulations were initiated (Figure 1c,d). Lastly, patterns in the estimated abundances of juvenile (<150 mm TL) and adult smallmouth bass (Table 2) combined with age-structure and estimates of natural survival (Table 1) indicated greater potential recruitment levels in Elkhead compared to Ridgway, which was reflected in the stock-recruitment relationships (Figure 1g,h).

The harvest rates of adult smallmouth bass achieved by anglers were lower in Elkhead (0.151-0.204) than in Ridgway (0.218-0.516), but effective fishing effort was also lower in Elkhead (560-631 hours) compared to Ridgway (1,937-2,194 hours). This included 2016, when tournament duration and timing (9 days in June) was the same for both reservoirs, before tournament timing in Ridgway shifted to July with a duration of 24 days in 2017. Lower effort levels were observed in Elkhead despite a greater number of registered anglers (269-332) when compared to Ridgway (123-211; Table 2). However, anglers fishing Elkhead in June were more effective than anglers fishing Ridgway in June and July across a similar range of smallmouth bass population densities, based on age-specific estimates of catchability standardized to 1,000 hours of effective effort (Figure 1e). For Ridgway, anglers fishing during July 2017 were more effective than June 2016 (Figure 1e), despite nearly equal adult abundance and density at the start of each tournament (Table 1).

Short-term population responses

The short-term responses of adult smallmouth bass to annual fishing tournaments differed between reservoirs, but were sensitive to simulated effort and recruitment levels and whether catchability was fixed or inversely related to abundance (Figures 2 and 3). Under observed effort (596 ± 50 hours) and recruitment (Figure 1g) in Elkhead, the mean abundance of adult smallmouth bass stabilized and increased by 30-42% by year 30 under both fixed and inverse catchability (Figure 2a,b). Angler harvest rates were not sufficient to overcome recruitment and suppress the Elkhead population in these simulations. Instead, the population achieved a higher long-term equilibrium abundance around 3,000 adults and a minimal effect of inverse catchability was observed. Conversely, the abundance of adult smallmouth bass in Ridgway decreased by 90-99% depending on catchability (Figure 2e,f) under observed effort (2,066 ± 182 hours) and recruitment (Figure 1h). Harvest rates were sufficient to cause overfishing and population suppression, particularly when assuming inverse catchability (Figure 2f).

Exchanging the effort and recruitment levels (i.e., applying observed values from Elkhead to Ridgway and vice versa) generated opposite patterns in short-term population trajectories. Under higher effort levels reflective of Ridgway, the mean abundance of adult smallmouth bass in Elkhead decreased by 63-99% by year 30 depending on catchability (Figure 2c,d). Under lower effort levels reflective of Elkhead, the abundance of adult smallmouth bass in Ridgway declined, but stabilized around 3,000 adults (Figure 2g,h). Under lower recruitment levels reflective of Ridgway, anglers could reduce the adult smallmouth bass population in Elkhead by 31-65% depending on catchability at observed effort levels, but abundance stabilized around 750-1,500 adults (Figure 3c,d). A similar pattern emerged for Ridgway under observed effort assuming higher recruitment levels reflective of Elkhead and fixed catchability (Figure 3g). Assuming inverse catchability, anglers could overcome greater recruitment and suppress the adult population in Ridgway by 99% over the simulation period (Figure 3h).

Long-term equilibrium dynamics

Threshold values for the annual effective fishing effort and corresponding adult harvest rate required to achieve long-term unsustainability varied between reservoirs, and were sensitive to assumptions underlying catchability and recruitment (Figure 4). In Elkhead, the model indicated that an annual average of 2,568 hours of effort (4-fold higher than observed) were needed to drive the adult smallmouth bass population to low levels over the long-term assuming fixed catchability and observed recruitment, but only 1,093 hours assuming inverse catchability (Figure 4a). These effort levels translated into an annual adult harvest rate of 70% (Figure 4c). These values declined considerably to 1,584 hours, 674 hours, and 52%, respectively, after assuming lower recruitment levels reflective of Ridgway (Figure 4a,c). In Ridgway, the model indicated that an annual average of 1,963 hours (similar to observed) were needed to drive the population to low levels assuming fixed catchability and observed recruitment, but only 838 hours assuming inverse catchability (Figure 4b). These effort levels translated into an annual adult harvest rate of 43% (Figure 4d). These values increased to 2,659 hours, 1,308 hours, and 54%, respectively, after assuming higher recruitment levels reflective of Elkhead (Figure 4b,d).

Sensitivity analysis

Model outcomes from each reservoir were sensitive to similar parameter sets governing the vital rates of each population. In Elkhead, abundance at year 30 (N_{30}) was most sensitive to 10% reductions in maximum average TL (L_∞), ±10% changes in natural survival (S), and ±10% changes in maximum recruits per spawner (α; Table 3). Changes to S, however, generated the greatest changes in N_{30}. For example, increasing S by 10% from 0.648 to 0.713 increased N_{30} by 34.1% from 3,014 to 4,043 adults. In Ridgway, increasing S by 10% from 0.735 to 0.809 increased N_{30} by 174.5% from 480 to 1,318 adults (Table 4). Unlike Elkhead, N_{30} in Ridgway was also sensitive to parameters governing the size-dependent maturity schedule (β_0 and β_1) for males and females. Changes of ±10% in these parameters changed N_{30} by ±47.0-61.8%. If changes increased the proportion of fish mature at smaller body sizes, then N_{30} increased and vice versa.

Threshold fishing effort levels ($E_{\min}$) and adult harvest rates (μ_{adult}) needed to achieve unsustainability were sensitive to parameters governing growth, maturity, survival, and recruitment in each reservoir (Tables 3 and 4). Similar to N_{30}, threshold values were sensitive to ±10% changes in S. Reductions of 10% in S decreased threshold values by 21.2-34.0% across reservoirs. Conversely, 10% increases in S increased threshold values by 16.8-30.2%. Threshold values were generally more sensitive to changes in growth and maturity parameters given codependence in these processes, particularly in Elkhead. For example, ±10% changes in L_∞ or K generated ±25.4-76.0% changes in E_{min} and μ_{adult} in Elkhead, but only ±20.0-33.1% changes in Ridgway (Tables 3 and 4). In general, changes to individual growth parameters that increased size-at-age (e.g., increasing L_∞ or K) enabled more rapid maturation, which generated populations more resilient to harvest. Populations exhibiting slower growth and/or more delayed maturation were easier for anglers to suppress in the model.

DISCUSSION

Integrating empirical measures of population demographics and harvest dynamics with model simulations demonstrated that incentivized anglers could control a common invasive freshwater predator under some circumstances. Although effort levels observed from Elkhead were not sufficient to reduce the abundance of smallmouth bass at estimated recruitment levels, notable reductions occurred at effort levels observed from Ridgway, especially assuming inverse catchability. Thus, strategies that increase effort such as recruiting more anglers through enhanced outreach programs, modifying incentive structures to best align with angler desires, or increasing tournament duration could increase efficacy. In addition, angler effectiveness varied between study systems, and was temporally-dynamic within the same system, which suggests opportunity to adapt tournament structure to increase harvest rates. For example, shifting tournament timing on Ridgway from June to July increased the catchability of younger fish by 2-fold or more. Elevating effort during periods that maximize the catchability of target fish could further increase success. Therefore, incentivized angling should not be dismissed as a potential control strategy alone or in tandem with other methods as part of an integrated invasive species management plan, particularly in smaller, closed systems. Our combined field monitoring and modeling framework can be used to explore how potential temporal shifts in population demographics and/or angler dynamics may alter outcomes and the resilience of target populations to harvest, thereby facilitating adaptive and informed control programs that foster continued research and understanding.

For invasive fishes, there has been relatively little research on the control of nuisance smallmouth bass, and numerous potential control methods including incentivized harvest have remained untested (Loppnow et al., 2013). The few documented attempts to remove smallmouth bass through non-incentivized harvest were considered inappropriate when compared to other methods (Boucher, 2006; Gomez & Wilkinson, 2008). As a result, researchers have largely dismissed non-incentivized harvest as a viable control method, but some acknowledge that harvest alone could be effective in smaller systems where fishing pressure is high (Carey et al., 2011; Loppnow et al., 2013). Some programs have employed direct removals through boat electrofishing given its effectiveness at capturing nearshore fishes (Weidel et al., 2007; Hawkins et al., 2009; Loppnow et al., 2013; Breton et al., 2015). However, this method has also been criticized since increases in recruitment were observed following treatment in the few documented cases evaluated rigorously (Weidel et al., 2007; Hawkins et al., 2009). Like angling, boat electrofishing generally removes more adult fish than juveniles, and as a result, may elevate recruitment by reducing intraspecific competition and improving the survival and/or accelerating the maturation of juveniles (Zipkin et al., 2008; Loppnow et al., 2013). In these cases, removal efforts targeting juveniles, particularly young-of-year fish, in addition to highly fecund adults may be required to achieve control program goals (Loppnow & Venturelli, 2014).

Mechanical removal of invasive smallmouth bass from Little Moose Lake, New York, USA resulted in the proliferation of juvenile fish, and is a well-documented case study of how high harvest rates may lead to unintended outcomes in invasive species management (Zipkin et al., 2009). There, boat electrofishing removals reduced the catch rates of adult smallmouth bass by 90% after two years, and the native littoral fish community and food web recovered rapidly (Lepak et al., 2006; Weidel et al., 2007). However, strong year classes of fish were observed thereafter, and despite ongoing removal efforts, catch rates of juveniles increased to levels suggesting that population abundance as a whole increased post-treatment (i.e., "hydra effect" or "overcompensation"; Zipkin et al., 2008, 2009). Exploitation can cause compensatory responses in population demographics if reductions in abundance lessen negative density dependence. Such responses increase resilience to harvest or create overcompensatory or chaotic population dynamics (Rose et al., 2001; Zipkin et al., 2009; Syslo et al., 2011). However, biological processes such as recruitment can be complex (Ridgway et al., 1991; Gross & Kapuscinski, 1997; Ridgway et al., 2002), and simulations from Elkhead and Ridgway suggest that it may be prudent to conduct additional empirical removal studies before generalizing how invasive smallmouth bass or other fishes respond to harvest. Processes governing populations in other regions or ecosystems could differ from the few rigorously studied smallmouth bass populations experiencing intensive harvest.

While preliminary field and modeling results from this study show potential for incentivized harvest to be an effective control strategy in some cases, we acknowledge that these findings were derived from responses observed at the onset of new programs and their overall success remains to be seen. Our model simulations depended on two key assumptions. First, we assumed that relatively high angler effort would remain stable over the simulation period.

However, participation could wane as perceived fishery quality declines (Beard et al., 1997; Schueller et al., 2012; Askey & Johnston, 2013), unless outreach programs or incentives remain strong enough to attract and retain participants. Although, it is possible that processes such as inverse density-dependent catchability (as demonstrated in our model) could maintain high catch rates (considered desirable by many anglers) and buffer incentive programs from reduced participation (Johnson & Carpenter, 1994; Post et al., 2002; Hunt et al., 2011). Second, we assumed that vital rates would not exhibit compensatory responses with declines in population density. We wanted to develop a relatively simple model informed by empirical data that could generate baseline hypotheses to facilitate continued research and applicability in new test systems, rather than assuming overcompensation would occur *a priori*. Instead, we conducted a local sensitivity analysis which demonstrated how changes in the interactive processes of growth, maturation, recruitment, and survival could increase resilience to harvest within the range of demographics characterizing our smallmouth bass populations. Further empirical removals and monitoring are required to fully document responses and evaluate the appropriateness of model assumptions (Zipkin et al., 2009; Simberloff, 2009, 2021).

There is uncertainty in how our target populations might respond to continued harvest, but some system attributes could mediate the potential for undesirable outcomes. First, our study systems were small, highly fluctuating reservoirs, which may have lower ecological capacity to support overcompensatory responses compared to larger, more stable ecosystems (Post et al., 2000; Hansen et al., 2018). Water level fluctuations on the scale of meters to tens of meters (as observed in our systems) can degrade benthic-littoral habitat complexity and biotic communities that support upper trophic level consumers, particularly nearshore fishes like smallmouth bass (Weidel et al., 2000; Evtimova & Donahue, 2016; Hansen et al., 2018). Climate-driven reductions in water levels and extended periods or severity of drought could heighten adverse interactions with other top predators in the treated system (Hansen et al., 2022), especially in artificial systems like ours that often support novel fish assemblages and crowded trophic niche spaces (Winters & Budy, 2015). Further, periods of low water levels could enhance the effectiveness of control programs by concentrating invasive fishes and making them more vulnerable to anglers, but drier conditions can also negatively affect the treated aquatic ecosystem, which could be a disproportionate detriment to native species and biodiversity (Pearson et al., 2022). Lastly, interactions among water level fluctuations and other abiotic and biotic factors can influence recruitment in complex ways. Fluctuations could limit or enhance the productivity of fishes that spawn and rear nearshore depending on how the direction, timing and extent of fluctuations interact with other ecological factors and align with the life-history or phenological requirements of species. These interactions are particularly relevant to shallow water nest builders like smallmouth bass (Clark et al., 2008).

Implementing control programs early in the invasion process (i.e., rapid detection and response) can enhance the chances of meeting program goals (Dunham et al., 2020; Reaser et al., 2020). This notion is relevant to smallmouth bass as their productivity can vary temporally depending on the stage of invasion. For example, in Lake Opeongo, the abundance of adult fish and recruitment levels remained low for ~50 years post-introduction (“establishment” phase), then increased rapidly to peak levels approximately 4-fold higher (“expansion” phase) over the following two decades, before dropping to intermediate levels as the population equilibrated within the ecosystem (“accommodation” phase; Shuter & Ridgway, 2002). In Little Moose Lake, smallmouth bass were introduced at least 6 decades prior to removals. Given the invasion timeline observed in Lake Opeongo, smallmouth bass in Little Moose Lake could have been in a more advanced invasion phase that facilitated overcompensation after extensive removal of adults. Yet, in Lake Opeongo, low numbers of spawning adults (i.e., ≤20% of the maximum abundance observed across the 58-year time series) produced low numbers of recruits independent of invasion phase (Shuter & Ridgway, 2002). This pattern is contrary to expectations based on observations from Little Moose Lake, and suggests that the potential for overcompensation following large reductions in adult fish from harvest or other processes depends on system-specific factors.

The rate and extent of population expansions for introduced species can depend on a host of time-varying ecological factors and be scale-dependent (Pintor & Sih, 2011; Havel et al., 2015). As a result, expansions and effects on ecosystems can occur rapidly and exponentially at one extreme, or stay below detection limits for prolonged periods (Crooks & Soule, 1999; Crooks, 2005). Smallmouth bass have been present in our study systems for shorter periods than in Lake Opeongo or Little Moose Lake. This was particularly apparent in Ridgway (removals initiated an estimated 7 years post-reporting), which exhibited a more fragmented and truncated age structure when compared to Elkhead (35 years post-stocking). However, given the complexity of invasion dynamics, it is difficult to determine whether our populations were within a relatively low- or high-productivity regime when control programs began. Therefore, we assumed that each population was at an intermediate adult abundance level where average recruitment is at its peak according to density-dependent Ricker dynamics (Zipkin et al., 2008). This assumption was supported based on similarities in the abundance of at least 50% mature smallmouth bass (fish age-3+) observed in our systems versus the abundance of at least 50% mature smallmouth bass (fish age-5+) where peak recruitment levels were observed in Lake Opeongo (Shuter & Ridgway, 2002). In addition, peak recruitment levels (and variation) estimated in Elkhead were higher than in Ridgway, which aligned with expectations based on differences in the timelines of invasion. That said, the stock-recruitment relationships derived here are conceptual, and should be interpreted as working hypotheses to help anticipate and understand empirical observations.

CONCLUSIONS

In this study, we field tested and modeled the potential biological effectiveness of a conventional approach to invasive species management (i.e., population control through direct removals) using an unconventional or largely untested method (i.e., incentivized harvest alone). Model results showed promise at the scale of our study systems, but were contingent on simplifying assumptions related to program participation, density-dependent responses by target smallmouth bass populations, and the potential for overcompensation. However, such assessments are important for first evaluating feasibility of removal efforts and facilitating continued research and empirical data collection. This notion is particularly relevant to the management of invasive smallmouth bass where peer-reviewed literature has relied heavily on the evaluation of smallmouth bass removal in a single system where an undesirable response (an increase in smallmouth bass) was observed (i.e., Zipkin et al., 2009).

We acknowledge that control efforts are not always a desirable option, especially when invaders are considered “here to stay” or “out of control”. In this situation, alternative methods that focus on the mitigation of impacts by manipulating other endogenous or exogenous factors may be more appropriate (Dunham et al., 2020). For example, smallmouth bass have established widely in river systems of the western United States (Carey et al., 2011), and consumption of native fish is of primary concern (Lawrence et al., 2015). Successful control through removals brings extensive challenges given the large size and open-nature of the invaded ecosystems and social-ecological tensions with anglers (Loppnow et al., 2013; Rahel & Smith, 2018). Managing for cooler thermal regimes if possible to favor natives might be more appropriate (Rubenson & Olden, 2017; Dunham et al., 2020).

Control was deemed an appropriate approach given the small scale and closed-nature of our study systems, the presence of infrastructure to limit escapement of fish to sensitive riverine habitats downstream, and other program objectives related to public perceptions. We confronted long-standing and nuanced social-ecological tensions with anglers by providing harvest incentives and using the tournaments as a platform for outreach and education. Such platforms may be useful for reducing unauthorized introductions at local and regional scales and shifting social perceptions to be more inclusive of native biodiversity (Johnson et al. 2009). The latter is considered a key element in the management of socially-valued, but ecologically-detrimental aquatic invaders (Rahel & Smith, 2018), and could be integrated with emerging, unconventional approaches to invasive species management at broader landscape scales (Dunham et al., 2020).

ACKNOWLEDGMENTS

We thank current and former Colorado Parks and Wildlife employees and staff for contributions to data and sample collection as well as permissions and project input. We thank the reviewers of this research for their critiques and contributions to improve the manuscript. Project support and funding was provided by Colorado Parks and Wildlife.

REFERENCES

Adams J. V., O. Bircean, W. L. Chadderton, M. L. Jones, J. M. Lepak, T. S. Seilheimer, T. B. Steeves, W. P. Sullivan, and J. Wingfield. 2021. Trade-offs between Suppression and Eradication of Sea Lampreys from the Great Lakes *Journal of Great Lakes Research* 47: 782–95.

Aday, D. D., J. J. Parkos III, and D. H. Wahl. 2009. In *Centrarchid Fishes: Diversity, Biology, and Conservation*, edited by S. Cooke, and D. P. Philipp. Chichester, United Kingdom: Wiley–Blackwell Publishing.

Askey, P. J., and N. T. Johnston. 2013. Self-regulation of the Okanagan Lake Kokanee Recreational Fishery: Dynamic Angler Effort Response to Varying Fish Abundance and Productivity. *North American Journal of Fisheries Management* 33: 926–39.

Bayley, P. B., and D. J. Austen. 2002. Capture Efficiency of a Boat Electrofisher. *Transactions of the American Fisheries Society* 131: 435–51.

Beamesderfer, R. C. P., and J. A. North. 1995. Growth, Mortality, and Predicted Response to Fishing for Largemouth Bass and Smallmouth Bass Populations in North America. *North American Journal of Fisheries Management* 15: 688–704.

Beamesderfer, R. C. P., and B. E. Reiman. 1988. Size Selectivity and Bias in Estimates of Population Statistics of Smallmouth Bass, Walleye, and Northern Squawfish in a Columbia River Reservoir. *North American Journal of Fisheries Management* 8: 505–10.

Beard, T. D., Jr., S. W., Hewett, Q. Yang, R. M. King, and S. J. Gilbert. 1997. Prediction of Angler Catch Rates Based on Walleye Population Density. *North American Journal of Fisheries Management* 17: 621–27.

Boucher, D. P. 2005. *Rapid River and Pond in the River Fisher Investigations*. *Report No. 05-1*. Maine: Maine Department of Inland Fisheries and Wildlife.

Breton, A. R., J. A. Hawkins, K. R. Bestgen, D. L. Winkelman, and G. C. White. 2013. *Escapement of Translocated Smallmouth Bass (Micropterus dolomieu) from Elkhead Reservoir to the Yampa River*. Fort Collins, CO: Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado.

Breton, A. R., D. L. Winkelman, K. R. Bestgen, and J. A. Hawkins. 2015. *Population Dynamics Modeling of Introduced Smallmouth Bass in the Upper Colorado River Basin*. Fort Collins, CO: Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado.

Carey, M. P., B. L. Sanderson, T. A. Friesen, K. A. Barnas, and J. D. Olden. 2011. Smallmouth Bass in the Pacific Northwest: A Threat to Native Species; A Benefit for Anglers. *Reviews in Fisheries Science* 19: 305–15.

Clarke, M. E., K. A. Rose, J. A. Chandler, T. J. Richter, D. J. Orth, and W. Van Winkle. 2008. Water-Level Fluctuation Effects on Centrarchid Reproductive Success in Reservoirs: A Modeling Analysis. *North American Journal of Fisheries Management* 28: 1138–56.

Costantino, R. F., R. A. Desharnais, J. M. Cushing, and B. Dennis. 1997. “Chaotic Dynamics in an Insect Population.” *Science* 275: 389–91.

Cowx, I. G., R. Arlinghaus, S. J. Cooke. 2010. Harmonizing Recreational Fisheries and Conservation Objectives for Aquatic Biodiversity in Inland Waters. *Journal of Fish Biology* 76: 2194–2215.

Crooks, J. A. 2005. Lag Times and Exotic Species: The Ecology and Management of Biological Invasions in Slow-Motion. *Ecoscience* 12: 316–29.

Crooks, J. A., and M. E. Soule. 1999. In *Invasive Species and Biodiversity Management*, edited by O. T. Sandlund, P. J. Schei, and A. Viken. Boston, MA: Kluwer Academic Publishers.

Dunham, J. B., I. Arismendi, C. Murphy, A. Koeberle, J. A. Olivos, J. Peasrson, F. Pickens, D. Roon, and J. Stevenson. 2020. What to Do When Invaders are Out of Control? *WIREs Water* 7: e1476.

Dungeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater Biodiversity: Importance, Threats, Status and Conservation Challenges. *Biological Reviews* 81: 163–82.

Duron, Q., A. B. Shiels, and E. Vidal. 2017. Control of Invasive Rats on Islands and Priorities for Future Action. *Conservation Biology* 31: 761–71.

Dux, A. M., M. J., Hansen, M. P., Corsi, N. C. Wahl, J. P. Fredericks, C. E. Corsi, D. J. Schill, and N. J. Horner. 2019. Effectiveness of Lake Trout (*Salvelinus namaycush*) Suppression in Lake Pend Oreille, Idaho: 2006-2016. *Hydrobiologia* 840: 319–33.

Evtimova, V. V., and I. Donohue. 2016. Water-level Fluctuations Regulate the Structure and Functioning of Natural Lakes. *Freshwater Biology* 61: 251–64.

Gomez, L., and T. Wilkinson. 2008. *A Preliminary Assessment of Smallmouth Bass in the Beaver Creek System 2007–2008*. Borland Williams Lake, BC: British Columbia Ministry of Environment, Cariboo Region.

Gozlan, R. E., D. Burnard, D. Andreou, and J. R. Britton. 2013. Understanding the Threats Posed by Non-Native Species: Public vs. Conservation Managers. *PLoS One* 8: e53200.

Gross, M. L., and A. R. Kapuscinski. 1997. Reproductive Success of Smallmouth Bass Estimated and Evaluated from Family-Specific DNA Fingerprints. *Ecology* 78: 1424–30.

Hansen, A. G., J. R. Gardner, K. A. Connelly, M. Polacek, and D. A. Beauchamp. 2018. Trophic Compression of Lake Foods Webs under Hydrologic Disturbance. *Ecosphere* 9: e02304.

Hansen, A. G., J. R. Gardner, K. A. Connelly, M. Polacek, and D. A. Beauchamp. 2022. Resource Use among Top-Level Piscivores in a Temperate Reservoir: Implications for a Threatened Coldwater Specialist. *Ecology of Freshwater Fish* 31: 469–91.

Hansen, M. J., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid Predator-Prey Dynamics in Lake Pend Orielle, Idaho, USA. *Hydrobiologia* 650: 85–100.

Havel, J. E., K. E. Kovalenko, S. M. Thomaz, S. Amalfitano, and L. B. Kats. 2015. Aquatic Invasive Species: Challenges for the Future. *Hydrobiologia* 750: 147–70.

Hawkins, J., C. Walford, and A. Hill. 2009. *Smallmouth Bass Control in the Middle Yampa River, 2003–2007*. *Report No. 125*. Lakewood, CO: Upper Colorado River Endangered Fish Recovery Program, U.S. Fish and Wildlife Service.

Hayes, D. B., J. R. Bence, T. J. Kwak, and B. E. Thompson. 2007. In *Analysis and Interpretation of Freshwater Fisheries Data*, edited by C. S. Guy, and M. L. Brown. Bethesda, MD: American Fisheries Society.

Healy, B. D., E. C. Omana Smith, R. C. Schelly, M. A. Trammell, and C. B. Nelson. 2020. Establishment of a Reproducing Population of Endangered Humpback Chub through Translocations to a Colorado River Tributary in Grand Canyon, Arizona. *North American Journal of Fisheries Management* 40: 278–92.

Holmes, N. D., K. J. Campbell, B. S. Keitt, R. Griffiths, J. Beek, C. J. Donlan, and K. G. Broome. 2015. Reporting Costs for Invasive Vertebrate Eradications. *Biological Invasions* 17: 2913–25.

Hunt, L. M., R. Arlinghaus, N. Lester, and R. Kushneriuk. 2011. The Effects of Regional Angling Effort, Angler Behavior, and Harvesting Efficiency on Landscape Patterns of Overfishing. *Ecological Applications* 21: 2555–75.

Isely, J. J., and T. B. Grabowski. 2007. In *Analysis and Interpretation of Freshwater Fisheries Data*, edited by C. S. Guy, and M. L. Brown. Bethesda, MD: American Fisheries Society.

Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are We Doing all We Can to Stem the Tide of Illegal Fish Stocking? *Fisheries* 34: 389–94.

Johnson, P. T. J., J. D. Olden, and M. J. Vander Zanden. 2008. Dam Invaders: Impoundments Facilitate Biological Invasions into Freshwaters. *Frontiers in Ecology and the Environment* 6: 357–63.

Jones, M. L., and J. V. Adams. 2021. Eradication of Sea Lampreys from the Laurentian Great Lakes is Possible. *Journal of Great Lakes Research* 47: 776–81.

Kirk, M. A., B. M. Maitland, B. T. Hickerson, A. W. Walters, and F. J. Rahel. 2022. Climatic Drivers and Ecological Impacts of a Rapid Range Expansion of Non-Native Smallmouth Bass. *Biological Invasions* 24: 1311–26.

Khosa, D., S. M. Marr, R. J. Wasserman, T. A. Zengeya, and O. L. F. Weyl. 2019. An Evaluation of the Current Extent and Potential Spread of Black Bass Invasion in South Africa. *Biological Invasions* 21: 1721–36.

Koenig, M. K., K. A. Meyer, J. R. Kozfkay, J. M. Dupont, and E. B. Schriever. 2015. Evaluating the Ability of Tiger Muskellunge to Eradicate Brook Trout in Idaho Alpine Lakes. *North American Journal of Fisheries Management* 35: 659–70.

Lawrence, D. J., D. A. Beauchamp, and J. D. Olden. 2015. Life-Stage-Specific Physiology Defines Invasion Extent of a Riverine Fish. *Journal of Animal Ecology* 84: 879–88.

Lepak, J. M., C. E. Kraft, and B. C. Weidel. 2006. Rapid Food Web Recovery in Response to Removal of an Introduced Apex Predator. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 569–575.

Loppnow, G. L., K. Vascotto, and P. A. Venturelli. 2013. Invasive Smallmouth Bass (*Micropterus dolomieu*): History, Impacts, and Control. *Management of Biological Invasions* 4: 191–206.

Loppnow, G. L., and P. A. Venturelli. 2014. Stage-Structured Simulations Suggest That Removing Young of the Year is an Effective Method for Controlling Invasive Smallmouth Bass. *Transactions of the American Fisheries Society* 143: 1341–47.

Martinez, P. J., K. Wilson, P. Cavalli, H. Crockett, D. Speas, M. Trammell, B. Albrecht, and D. Ryden. 2014. *Upper Colorado River Basin Nonnative and Invasive Aquatic Species Prevention and Control Strategy*. Upper Colorado River Endangered Fish Recovery Program.

Miranda, L. E., and P. W. Bettoli. 2007. In *Analysis and Interpretation of Freshwater Fisheries Data*, edited by C. S. Guy, and M. L. Brown. Bethesda, MD: American Fisheries Society.

Mueller, G. A. 2005. Predatory Fish Removal and Native Fish Recovery in the Colorado River Mainstem: What have We Learned? *Fisheries* 30: 10–19.

Pardini, E. A., J. M. Drake, J. M. Chase, and T. M. Knight. 2009. Complex Population Dynamics and Control of the Invasive Biennial *Alliaria petiolata* (Garlic Mustard). *Ecological Applications* 19: 387–97.

Pearson, J. B., J. R. Belmore, and J. B. Dunham. 2022. Controlling Invasive Fish in Fluctuating Environments: Model Analysis of Common Carp (*Cyprinus carpio*) in a Shallow Lake. *Ecosphere* 13: e3985.

Pearson, J. B., J. B. Dunham, J. R. Belmore, and D. Lyons. 2019. Modeling Control of Common Carp (*Cyprinus carpio*) in a Shallow-Lake Wetland System. *Wetlands Ecology and Management* 27: 663–82.

Peterman, R. M., and G. J. Steer. 1981. Relation between Sport-Fishing Catchability Coefficients and Salmon Abundance. *Transactions of the American Fisheries Society* 110: 585–93.

Pintor, L. M., and A. Sih. 2011. Scale Dependent Effect of Native Prey Diversity, Prey Biomass and Natural Disturbance on the Invasion Success of an Exotic Predator. *Biological Invasions* 13: 1357–66.

Post, D. M., M. L. Pace, and N. G. Hairston Jr. 2000. Ecosystem Size Determines Food-Chain Length in Lakes. *Nature* 405: 1047–49.

Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's Recreational Fisheries: The Invisible Collapse? *Fisheries* 27: 6–17.

Quinn, T. J., and R. B. Deriso. 1999. *Quantitative Fish Dynamics*. New York, NY: Oxford University Press.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available: http://www.Rproject.org. Accessed 16 August 2022.

Rahel, F. J. 2000. Homogenization of Fish Faunas across the United States. *Science* 288: 854–56.

Rahel, F. J., and M. A. Smith. 2018. Pathways of Unauthorized Fish Introductions and Types of Management Responses. *Hydrobiologia* 817: 41–56.

Reaser, J. K., S. W., Burgiel, J. Kirkey, K. A. Brantley, S. D. Veatch, and J. Burgos-Rodriguez. 2019. The Early Detection of and Rapid Response (EDRR) to Invasive Species: A Conceptual Framework and Federal Capacities Assessment. *Biological Invasions* 22: 1–19.

Ricker, W. E. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations. Bulletin 191*. Nanaimo, BC: Department of the Environment, Fisheries and Marine Service.

Ridgway, M. S., B. J. Shuter, and E. E. Post. 1991. The Relative Influence of Body Size and Territorial Behaviour on Nesting Asynchrony in Male Smallmouth Bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Journal of Animal Ecology* 60: 665–81.

Ridgway, M. S., B. J. Shuter, T. A. Middel, and M. L. Gross. 2002. Spatial Ecology and Density-Dependent Processes in Smallmouth Bass: The Juvenile Transition Hypothesis." *American Fisheries Society Symposium* 31: 47–60.

Rose, K. A., J. H. Cowan Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory Density Dependence in Fish Populations: Importance, Controversy, Understanding and Prognosis. *Fish and Fisheries* 2: 293–327.

Rubenson, E. S., and J. D. Olden. 2017. Dynamism in the Upstream Invasion Edge of a Freshwater Fish Exposes Range Boundary Constraints. *Oecologia* 184: 453–67.

Rytwinski, T., J. J. Taylor, L. A. Donaldson, J. R. Britton, D. R. Browne, R. E. Gresswell, M. Lintermans, K. A. Prior, M. G. Pellatt, C. Vis, and S. J. Cooke. 2019. The Effectiveness of Non-Native Fish Removal Techniques in Freshwater Ecosystems: A Systematic Review. *Environmental Reviews* 27: 71–94.

Schueller, A. M., A. H. Fayram, and M. J. Hansen. 2012. Simulated Equilibrium Walleye Population Density under Static and Dynamic Recreational Angling Effort. *North American Journal of Fisheries Management* 32: 894–904.

Seber, G. A. F. 1982. *The Estimation of Animal Abundance and Related Parameters*, *2nd Edition*. London, UK: Edward Arnold Publishers.

Shuter, B. J., J. E. Matuszek, and H. A. Regier. 1987. Optimal Use of Creel Survey Data in Assessing Population Behaviour: Lake Opeongo Lake Trout (*Salvelinus namaycush*) and Smallmouth Bass (*Micropterus dolomieu*), 1936–83. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 229–38.

Shuter, B. J., and M. S. Ridgway. 2002. In *Black Bass: Ecology, Conservation and Management*, edited by D. P. Philipp, and M. S. Ridgway. Bethesda, MD: American Fisheries Society.

Simberloff, D. 2009. We can Eliminate Invasions or Live with Them. Successful Management Projects. *Biological Invasions* 11: 149–57.

Simberloff, D., J. L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B. Galil, E. Garcia-Berthou, M. Pascal, P. Pysek, R. Sousa, E. Tabacchi, and M. Vila. 2013. Impacts of Biological Invasions: What's What and the Way Forward. *Trends in Ecology and Evolution* 28: 58–66.

Simberloff, D. 2021. Maintenance Management and Eradication of Established Aquatic Invaders. *Hydrobiologia* 848: 2399–2420.

Slipke, J. W., and M. J. Maceina. 2013. *Fishery Analysis and Modeling Simulator. Software Program Manual.* Bethesda, MD: American Fisheries Society.

Strayer, D. L., and D. Dudgeon. 2010. Freshwater Biodiversity Conservation: Recent Progress and Future Challenges. *Journal of the North American Benthological Society* 29: 344–58.

Syslo, J. M., C. S. Guy, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and T. M. Koel. 2011. Response of Non-Native Lake Trout (*Salvelinus namaycush*) to 15 years of Harvest in Yellowstone Lake, Yellowstone National Park. *Canadian Journal of Fisheries and Aquatic Sciences 68*: 2132–45.

Tiberti, R., T. Buchaca, D. Boiano, R. A. Knapp, Q. P. Rovira, G. Tavecchia, M. Ventura, and S. Tenan. 2021. Alien Fish Eradication from High Mountain Lakes by Multiple Removal Methods: Estimating Residual Abundance and Eradication Probability in Open Populations. *Journal of Applied Ecology 58*: 1055–68.

United States Census Bureau. 2016. *National Survey of Fishing, Hunting, & Wildlife-Associated Recreation (FHWAR): 2016*. Available: https://www.census.gov/library/publications/2018/demo/fhw-16-nat.html. Accessed 22 July 2022.

Vander Zanden, J. M., J. M. Casselman, and J. B. Rasmussen. 1999. Stable Isotope Evidence for the Food Web Consequences of Species Invasions in Lakes. *Nature* 401: 464–67.

Vander Zanden, J. M., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting Occurrences and Impacts of Smallmouth Bass Introductions in North Temperate Lakes. *Ecological Applications* 14: 132–48.

Warner, K. 2005. Smallmouth Bass Introductions in Maine: History and Management Implications. *Fisheries* 30: 20–36.

Weidel, B. C., D. C. Josephson, C. C. Krueger. 2000. Diet and Prey Selection of Naturalized Smallmouth Bass in an Oligotrophic Adirondack Lake. *Journal of Freshwater Ecology* 15: 411–20.

Weidel, B. C., D. C. Josephson, C. E. Kraft. 2007. Littoral Fish Community Response to Smallmouth Bass Removal from an Adirondack Lake. *Transactions of the American Fisheries Society* 136: 778–89.

Winters, L. K., and P. Budy. 2015. Exploring Crowded Trophic Niche Space in a Novel Reservoir Fish Assemblage: How Many is too Many? *Transactions of the American Fisheries Society 144*: 1117–28.

Wolff, B. A., B. M. Johnson, A. R. Breton, P. J. Martinez, and D. L. Winkelman. 2012. Origins of Invasive Piscivores Determined from the Strontium Isotope Ratio (^{87}Sr/^{86}Sr) of Otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 724–39.

Zipkin, E. F., P. J. Sullivan, E. G. Cooch, C. E. Kraft, B. J. Shuter, and B. C. Weidel. 2008. Overcompensatory Response of a Smallmouth Bass (*Micropterus dolomieu*) Population to Harvest: Release from Competition? *Canadian Journal of Fisheries and Aquatic Sciences* 65: 2279–92.

Zipkin, E. F., C. E. Kraft, E. G. Cooch, and P. J. Sullivan. 2009. When can Efforts to Control Nuisance and Invasive Species Backfire? *Ecological Applications* 19: 1585–95.

TABLES:

TABLE 1 Starting numbers-at-age and parameter values used for simulating the population dynamics of smallmouth bass in Elkhead and Ridgway reservoirs. For starting numbers-at-age, pre-tournament estimates from 2019 ($N_{a,2019}$) are listed for Elkhead and estimates from 2017 ($N_{a,2017}$) are listed for Ridgway. Values in the error columns for numbers-at-age represent 95% CIs. Where applicable, errors reported for all other estimated parameters are SEs except for Mean effort which are SDs used for simulation purposes. Age-classes not detected are indicated by an ND, but were simulated in the model.

	Elkhead Reservoir		Ridgway Reservoir	
Parameter	Estimate	Error	Estimate	Error
Starting numbers-at-age (last tournament in present series; 2019 and 2017)				
Age-1	3,518	1,609-5,519	2,116	1,644-2,586
Age-2	2,634	1,291-3,978	1,553	1,208-1,899
Age-3	1,228	889-1,567	2,520	2,089-2,951
Age-4	513	394-633	1,557	1,357-1,758
Age-5	218	167-269	440	385-494
Age-6	85	65-105	106	93-119
Age-7	36	27-44	77	67-86
Age-8	21	16-27	14	12-15
Age-9	7	5-8	0	-
Age-10	5	4-6	0	-
Age-11	7	5-8	8	7-9
Age-12	2	2-3	8	7-9
Age-13	5	4-7	ND	-
Age-14	3	2-3	ND	-
Age-15	0	-	ND	-
Age-16	0	-	ND	-
Age-17	ND	-	ND	-
Age-18	ND	-	ND	-
Effective fishing effort (total hours by tournament year)				
2017, 2015	Not recorded	-	Not recorded	-
2018, 2016	631	-	2,194	-
2019, 2017	560	-	1,937	-
Mean effort:	596	50	2,066	182
von Bertalanffy growth parameters (mm)				
L_∞	486.64	17.43	601.03	51.89
K	0.153	0.017	0.111	0.018
t_0	-0.295	0.248	0.182	0.198
Length-dependent probability of maturity (P_{male} and P_{female})				
β_0 (female)	-15.030	1.216	-18.057	1.072

β_1 (female)	0.073	0.006	0.088	0.005
β_0 (male)	-12.888	1.133	-16.124	1.014
β_1 (male)	0.080	0.007	0.105	0.007
Population sex ratio				
$Prop_f$	0.530	-	0.562	-
$Prop_m$	0.470	-	0.438	-
Catchability-at-age (q_a; scaled to 1,000 hours of effective effort)				
b_1 (June)	3.737	0.227	5.654	0.873
b_2 (June)	1.297	0.319	0.802	0.157
b_3 (June)	8.554	0.383	2.277	3.220
b_4 (June)	0.364	0.078	0.239	0.096
b_1 (July)	NA	-	3.891	0.555
b_2 (July)	NA	-	1.243	0.500
b_3 (July)	NA	-	4.558	1.388
b_4 (July)	NA	-	0.325	0.123
Mortality and natural survival				
Z	0.653	0.032	0.993	0.026
A	0.479	-	0.630	-
μ	0.128	-	0.365	-
v	0.352	-	0.265	-
S	0.648	0.016	0.735	0.010
Stock-recruitment (Ricker)				
α	3.243	-	2.408	-
β	0.000321	-	0.000418	-
σ	0.396	-	0.377	-

TABLE 2 Angler and mark-recapture summary for each tournament year in each study reservoir. All tournaments were conducted in early or mid-June, except for 2017 in Ridgway in which the tournament was conducted throughout July. Anglers represents the total number that registered for each tournament. Columns for n_1, n_2, and m_2 correspond to the Chapman estimator in equation (3). Values for n_2 also represent total bass harvest achieved during each tournament. Abundance estimates (Abund. est.) are parsed out by size-group (total length in mm) and CI represents confidence interval. Note that there was no attempt to mark bass 75-149 mm in 2015 on Ridgway. Corresponding size-dependent exploitation rates (proportion removed denoted by μ) are also provided. The acronym NR stands for "Not Recorded" and NE stands for "No Estimate." Values in parentheses are abundance estimates converted to a density (#/ha).

Reservoir	Year	Anglers	Effective effort (hours)	Size-group (mm)	n_1	n_2 (total harvest)	m_2	Abund. est.	Abund. ± 95% CI	μ	μ ± 95% CI
Elkhead	2017	332	NR	75-149	184	170	1	NE	-	-	-
				≥150	332	797	67	3,907 (10.7)	787	0.204	0.034
	2018	269	631	75-149	714	127	38	2,346 (6.4)	590	0.054	0.011
				≥150	626	413	94	2,731 (7.5)	442	0.151	0.021
	2019	270	560	75-149	315	89	9	2,843 (7.8)	1,559	0.031	0.011
				≥150	282	403	49	2,286 (6.3)	533	0.176	0.033
Ridgway	2015	211	NR	75-149	-	-	-	NE	-	-	-
				≥150	169	1,324	61	3,632 (9.3)	698	0.365	0.059
	2016	147	2,194	75-149	714	319	49	4,575 (11.7)	1,113	0.070	0.014
				≥150	310	821	67	3,758 (9.6)	751	0.218	0.036
	2017	123	1,937	75-149	290	533	54	2,824 (7.2)	631	0.189	0.034
				≥150	218	1,806	112	3,501 (8.9)	433	0.516	0.057

TABLE 3 Results from the sensitivity analysis evaluating the relative influence of model parameters governing vital rates for smallmouth bass in Elkhead Reservoir. Baseline values for the abundance of bass at simulation year 30 (N_{30}), the minimum annual fishing effort (total hours) required for achieving long-term unsustainability (E_{min}), and the corresponding minimum annual adult harvest rate (μ_{adult}; %) required for achieving long-term unsustainability were 3,014 adults (age-3+), 2,568 hours, and 70.2%, respectively. The parameters $Prop_f$ and $Prop_m$ were modified jointly to maintain a total proportion of 1.0. Values in bold highlight percent changes (%Δ) >10%.

	Parameter value – 10%						Parameter value + 10%					
	N_{30}		E_{min}		μ_{adult}		N_{30}		E_{min}		μ_{adult}	
Parameter	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ
L_∞	**2,657**	**-11.8**	**1,413**	**-45.0**	**47.8**	**-31.9**	3,068	1.8	**4,520**	**76.0**	**100.0**	**42.4**
K	2,782	-7.7	**1,606**	**-37.5**	**52.4**	**-25.4**	3,072	1.9	**3,910**	**52.3**	**96.0**	**36.7**
t_0	3,000	-0.5	2,439	-5.0	68.1	-3.0	3,026	0.4	2,703	5.3	72.3	3.0
β_0 (female)	3,063	1.6	**3,407**	**32.7**	**85.1**	**21.3**	2,908	-3.5	**1,986**	**-22.7**	**61.0**	**-13.1**
β_1 (female)	2,897	-3.9	**1,976**	**-23.1**	**60.8**	**-13.4**	3,061	1.5	**3,300**	**28.5**	**83.0**	**18.2**
β_0 (male)	3,072	1.9	**3,738**	**45.6**	**92.1**	**31.2**	2,906	-3.6	**1,884**	**-26.6**	**58.7**	**-16.4**
β_1 (male)	2,894	-4.0	**1,845**	**-28.2**	**57.8**	**-17.7**	3,069	1.8	**3,583**	**39.5**	**88.7**	**26.4**
$Prop_f$	3,033	0.6	2,778	8.2	73.6	4.8	2,990	-0.8	2,356	-8.3	66.8	-4.8
$Prop_m$	2,993	-0.7	2,380	-7.3	67.2	-4.3	3,031	0.6	2,754	7.2	73.2	4.2
S	**1,936**	**-35.8**	**1,783**	**-30.6**	**55.4**	**-21.2**	**4,043**	**34.1**	**3,235**	**26.0**	**82.0**	**16.8**
S (SE)	3,014	0.0	2,568	0.0	70.1	-0.1	3,014	0.0	2,568	0.0	70.1	-0.1
α	**2,627**	**-12.8**	**2,163**	**-15.8**	64.0	-8.8	**3,364**	**11.6**	**2,923**	**13.8**	76.1	8.3
β	**3,348**	**11.1**	2,568	0.0	70.2	0.0	2,741	-9.1	2,568	0.0	70.2	0.0
σ	2,972	-1.4	2,568	0.0	70.2	0.0	3,060	1.5	2,568	0.0	70.2	0.0

TABLE 4 Results from the sensitivity analysis evaluating the relative influence of model parameters governing vital rates for smallmouth bass in Ridgway Reservoir. Baseline values for the abundance of bass at simulation year 30 (N_{30}), the minimum annual fishing effort (total hours) required for achieving long-term unsustainability ($E_{\min}$), and the corresponding minimum annual adult harvest rate (μ_{adult}; %) required for achieving long-term unsustainability were 480 adults (age-3+), 1,963 hours, and 43.4%, respectively. The parameters $Prop_f$ and $Prop_m$ were modified jointly to maintain a total proportion of 1.0. Values in bold highlight percent changes (%Δ) >10%.

	Parameter value – 10%						Parameter value + 10%					
	N_{30}		$E_{\min}$		μ_{adult}		N_{30}		$E_{\min}$		μ_{adult}	
Parameter	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ	Value	%Δ
L_∞	**67**	**-86.0**	**1,314**	**-33.1**	**31.0**	**-28.6**	**961**	**100.2**	**2,605**	**32.7**	**53.6**	**23.3**
K	**98**	**-79.7**	**1,396**	**-28.9**	**32.7**	**-24.7**	**899**	**87.2**	**2,510**	**27.9**	**52.1**	**20.0**
t_0	510	6.1	1,999	1.8	43.9	1.0	451	-6.1	1,927	-1.8	42.6	-1.8
β_0 (female)	777	61.9	**2,330**	**18.7**	**49.3**	**13.6**	**255**	**-47.0**	**1,665**	**-15.2**	**37.9**	**-12.7**
β_1 (female)	**248**	**-48.3**	**1,654**	**-15.7**	**37.7**	**-13.2**	**740**	**54.1**	**2,280**	**16.1**	**48.5**	**11.7**
β_0 (male)	**728**	**51.6**	**2,284**	**16.4**	**48.6**	**11.9**	**200**	**-58.4**	**1,594**	**-18.8**	**36.6**	**-15.8**
β_1 (male)	**188**	**-60.8**	**1,576**	**-19.7**	**36.2**	**-16.6**	**710**	**47.7**	**2,258**	**15.0**	**48.2**	**10.9**
$Prop_f$	**581**	**21.1**	2,088	6.4	45.4	4.5	**385**	**-19.8**	1,845	-6.0	41.2	-5.2
$Prop_m$	**405**	**-15.6**	1,870	-4.7	41.6	-4.2	**559**	**16.3**	2,060	4.9	44.9	3.4
S	**94**	**-80.4**	**1,295**	**-34.0**	**29.7**	**-31.6**	**1,318**	**174.5**	**2,557**	**30.3**	**53.9**	**24.2**
S (SE)	480	0.0	1,963	0.0	43.4	0.0	480	0.0	1,963	0.0	43.4	0.0
α	**289**	**-39.8**	**1,745**	**-11.1**	39.4	-9.3	**721**	**50.0**	**2,173**	**10.7**	46.8	7.7
β	**529**	**10.1**	1,963	0.0	43.4	0.0	440	-8.4	1,963	0.0	43.4	0.0
σ	456	-5.1	1,963	0.0	43.4	0.0	508	5.7	1,963	0.0	43.4	0.0

FIGURES:

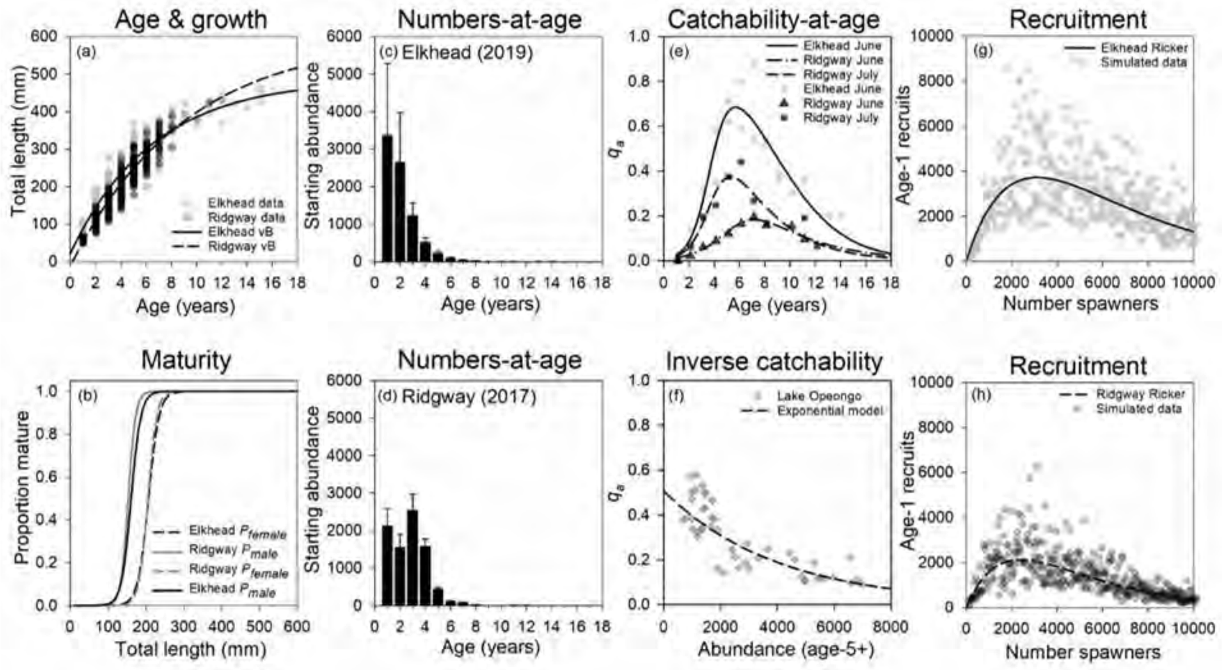

FIGURE 1 Primary model components. In panel (a), lines represent the fitted von-Bertalanffy (vB) growth functions to individual bass (points) donated by anglers from each reservoir. In panel (b), lines represent the fitted logistic regression models characterizing the probability of maturity as a function of length for male (P_{male}) and female (P_{female}) bass in each reservoir. In panels (c) and (d), error bars represent 95% confidence intervals. In panel (e), lines represent the double logistic functions (equation 7) fit to the corresponding observed catchabilities-at-age (q_a) for each month-reservoir combination (points). In panel (f), points represent empirical data from Lake Opeongo (Shuter et al. 1987), and the line represents equation (8) used to compute relative scaling factors for our study reservoirs. In panels (g) and (h), lines represent the deterministic Ricker stock-recruitment relationships approximated for bass in each reservoir. Points in these panels represent example simulated recruitment levels across the full range of spawner numbers based on recruitment variation estimated for bass in Lake Opeongo, Ontario, Canada (Shuter and Ridgway 2002).

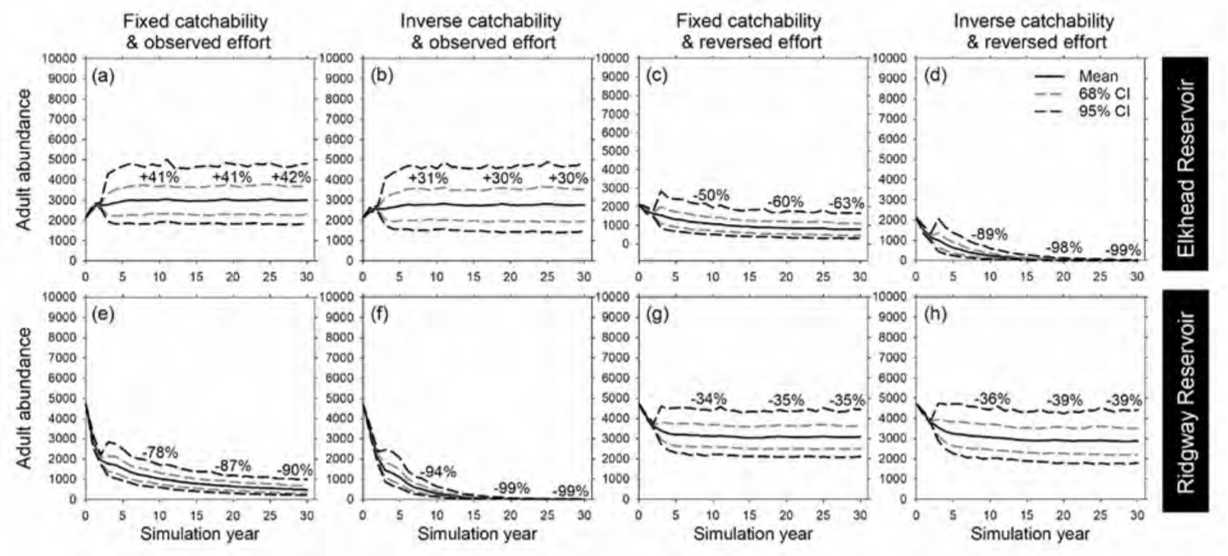

FIGURE 2 Simulated short-term population responses of adult (age-3+) smallmouth bass in Elkhead and Ridgway reservoirs to continuous harvest mortality derived from annual incentivized fishing tournaments. Simulations assumed either fixed (does not vary with abundance through time) or inverse (increases as abundance declines) catchability (system-specific) and either observed (system-specific) or exchanged (other system parameters) fishing effort levels in Elkhead (observed mean ± SD = 596 ± 50 hours for 9 days in late June) and Ridgway (2,066 ± 182 hours for 24 days through July). Values represent percent changes in mean abundance at simulation year 10, 20, and 30.

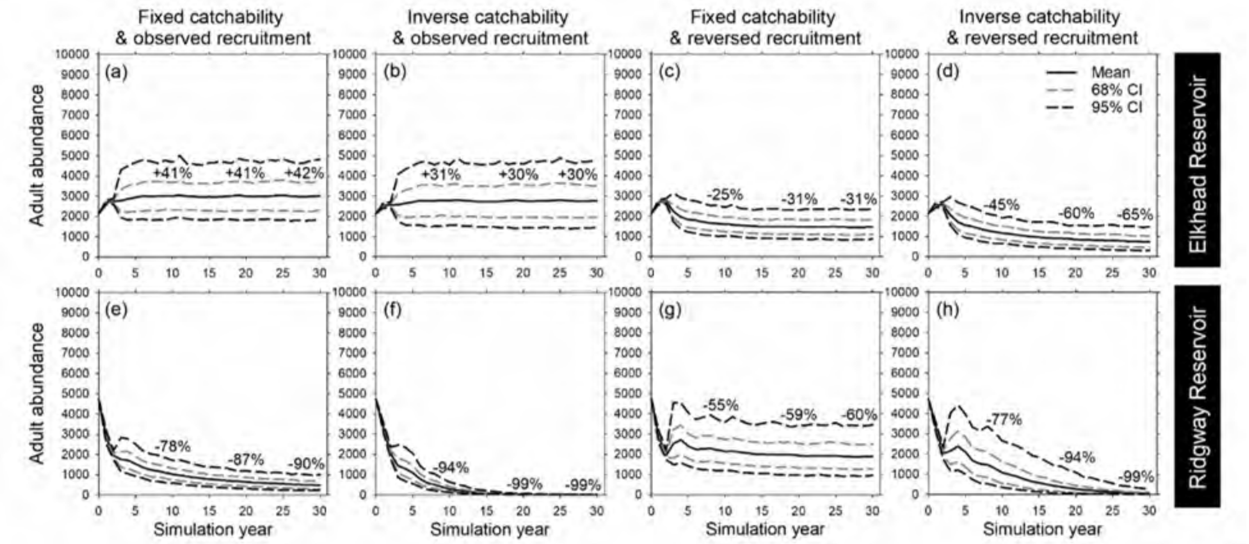

FIGURE 3 Simulated short-term population responses of adult (age-3+) smallmouth bass in Elkhead and Ridgway reservoirs to continuous harvest mortality derived from annual incentivized fishing tournaments. Simulations assumed either fixed (does not vary with abundance through time) or inverse (increases as abundance declines) catchability (system-specific), either observed (system-specific) or exchanged (other system parameters) recruitment dynamics in Elkhead ($\alpha = 3.243$, $\beta = 0.000321$, $\sigma = 0.396$) and Ridgway ($\alpha = 2.408$, $\beta = 0.000418$, $\sigma = 0.377$), and observed (system-specific) fishing effort levels. Values represent percent changes in mean abundance at simulation year 10, 20, and 30.

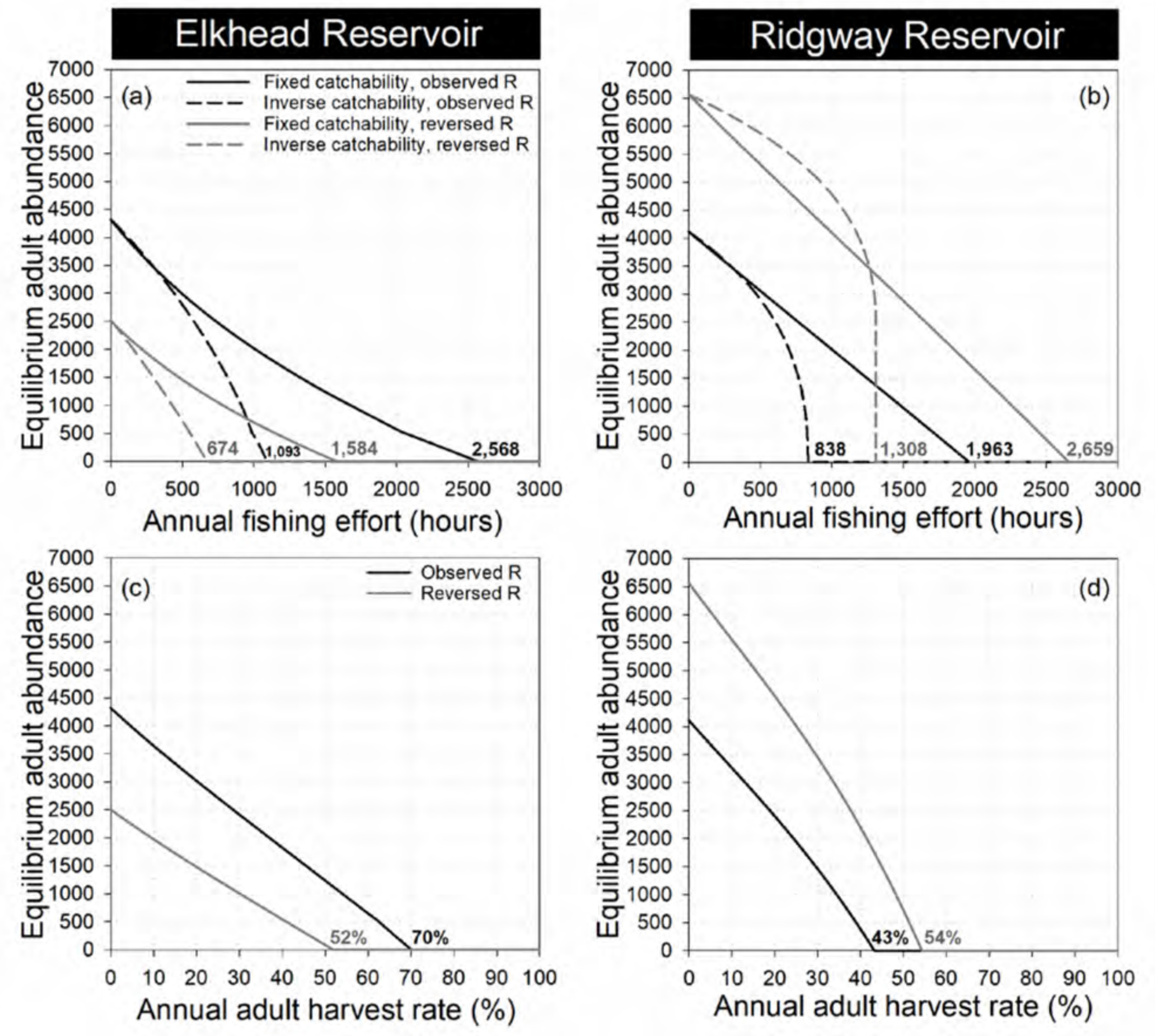

FIGURE 4 Simulated long-term equilibrium abundances of smallmouth bass in Elkhead (left panels) and Ridgway (right panels) reservoirs as a function of total annual fishing effort (top panels) and the corresponding annual adult (age-3+) harvest rate (bottom panels). Values denote threshold effort and harvest rates for achieving long-term unsustainability (i.e., where abundance is < 2.0 fish) under different assumptions of catchability (fixed or inverse) and recruitment (R; observed or exchanged parameters). Note that the relationship between equilibrium abundance and the annual adult harvest rate is not sensitive to assumptions underlying catchability (fixed or inverse).

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

OBJECTIVES

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

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

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

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

INTRODUCTION

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

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

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

A Research Associate was appointed through Colorado State University (CSU) within the Cooperative Fish and Wildlife Research Unit to address these issues from October 2022 to October 2023.

PROJECT PROGRESS

Shadow Mountain Reservoir

- Due to concerns about a Special Use Permit (SUP) from the Bureau of Reclamation, an amendment was developed for the project. The project amendment was completed, sent to Leadership, and was also sent to other states and approved with the stipulation of reporting the PIT tags used in Shadow Mountain Reservoir tiger muskellunge to the Recovery Program (already completed). The amendment describes an alternative PIT tag detection approach (Recovery Program antenna array and mobile surveys; Fetherman and Richer, CPW). PIT tag antennas are installed below Shadow Mountain Reservoir in the Colorado River, and these antennas were repaired/maintained and additional antennas were installed September 18th through the 21st. The CSU Research Associate assisted with maintenance and the installation of the new antenna arrays. This approach allowed for additional tiger muskellunge to be tagged versus what was originally proposed.

- From May 31st to June 1st, six overnight gill net sets with 150' experimental gear were completed. Approximately 75 WHS/LGS were collected per net. The Research Associate assisted with this survey.

- 5,400 tiger muskellunge intended for stocking in Shadow Mountain Reservoir were tagged with PIT tags at the CPW hatchery in Wray. Tagging was successful with low mortality, especially for tiger muskellunge originating from Pennsylvania (<0.3% mortality), while fish from Nebraska experienced higher tagging mortality (between 1 and 2%).

- On Sept. 14th, 13,000 tiger muskellunge were stocked into Shadow Mountain Reservoir. The Research Associate assisted with stocking and helped distribute the tiger muskellunge in protected areas with structure around the islands of Shadow Mountain Reservoir on the southern end.

Elkhead Reservoir

- In mid-April the Research Associate assisted CPW personnel with PIT and Floy tagging of tiger muskellunge at the Wray hatchery. These fish were stocked in Elkhead Reservoir and Harvey Gap Reservoir spring 2023 as larger "holdovers". On October 4th and 5th, 3,723 Floy tagged tiger muskellunge (approximately 7-inch fish) were stocked in Elkhead Reservoir. Of these fish, 100 individuals were held overnight October 4th to evaluate tag retention and survival. One individual had lost a tag by the morning of October 5th.

- Trapnets (5-6) were set in Elkhead Reservoir the nights of May 22nd to May 24th to capture and mark fish (Northern Pike specifically, but also Smallmouth Bass) for a population estimate based on fish turned in at the angling tournament intended to reduce numbers. The Research Associate assisted with this survey. Night electrofishing efforts were conducted June 12th and June 13th for the same purpose, but with more of a focus on Smallmouth Bass. The Research Associate assisted with these surveys.

- Northern Pike and Smallmouth Bass from the 2023 angling tournament in Elkhead Reservoir were collected and processed. These individuals will provide information about their abundance through time and their potential diet overlap with tiger muskellunge indicating the potential for competition.

Overall project components

- A Colorado-specific tiger muskellunge bioenergetics model was modified by coupling it with stocking data and a population dynamics (survival) model to estimate the age-specific energy demand of tiger muskellunge in terms of mass of White Sucker biomass. This was completed on all 117 systems stocked with tiger muskellunge to visualize potential impacts on target species.

- Data has been compiled from 56 reservoirs (of the 117 stocked with tiger muskellunge in Colorado from 1983 to 2023) with adequate information (i.e., consistent gear and effort metrics) to represent system-specific catch rates (CPUE) for fish species targeted by management actions (TGM stocking). Gear types, effort, nomenclature, and managers vary through time and across systems from 1983 to 2023. However, these systems have enough information to support further analyses.

- Monthly tiger muskellunge subsampling at the Wray Hatchery took place from May-August. Eye lenses from these individuals were dissected and samples have been prepared for analysis of carbon, nitrogen, and sulfur stable isotopes.

- Based on eye lens dissections, tiger muskellunge collected during sample periods 1 and 2, had developed 1-3 eye lens layers during their first several months after hatching. Tiger muskellunge from sample periods 3 and 4 had developed 4-7 eye lens layers since hatching. The cores of the eye lenses appeared to be relatively consistent near 400 to 500 microns. Full lens and core diameter measurements appear relatively consistent between the left and right eye, as well as between lab personnel.

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

OBJECTIVES

To prepare and submit a manuscript that identified factors at the landscape scale that are influencing mercury concentrations in Northern Pike, Smallmouth Bass, and Walleye. We also included an evaluation of theoretical changes in mercury deposition and food web structure to compare the magnitude and timing of potential changes in sport fish mercury concentrations from those changes.

PUBLICATION

Lepak, J. M., B. M. Johnson, M. B. Hooten, B. A. Wolff, and **A. G. Hansen.** 2023. Predictors of sport fish mercury contamination in heavily managed reservoirs: implications for human and ecological health. PLoS ONE 18(8):e0285890.

BACKGROUND

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

MANUSCRIPT ABSTRACT

Mercury (Hg) is an important contaminant due to its widespread distribution and tendency to accumulate to harmful levels in biota. We used a machine learning approach called random forest (RF) to evaluate different predictors of Hg concentrations in three species of Colorado sport fish. The RF approach indicated that the best predictors of large Northern Pike concentrations at 864 mm were covariates related to salmonid stocking in each study system, while system-specific metrics related more to productivity and forage base were the best predictors of Hg concentrations of Smallmouth Bass, and Walleye at 381 mm. Importantly,

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

REFERENCES

Wolff, B. A., B. M. Johnson, and J. M. Lepak. 2017. Changes in sport fish mercury concentrations from food web shifts suggest partial decoupling from mercury loading in two Colorado reservoirs. Archives of Environmental Contamination and Toxicology 72:167-177.

Lepak, J. M., M. B. Hooten, C. A. Eagles-Smith, M. T. Tate, M. A. Lutz, J. T. Ackerman, J. J. Willacker Jr., D. C. Evers, J. G. Wiener, C. Flanagan Pritz, and J. Davis. 2016. Assessing potential health risks to fish and humans using mercury concentrations in inland fish from across western Canada and the United States. Science of the Total Environment 571:342-354.

Johnson, B. M., J. M. Lepak, and B. A. Wolff. 2015. Effects of prey assemblage on mercury bioaccumulation in a piscivorous sport fish. Science of the Total Environment 506-507:330-337.

Lepak, J. M., M. B. Hooten, and B. M. Johnson. 2012a. The influence of external subsidies on diet, growth and Hg concentrations of freshwater sport fish: implications for fisheries management and the development of fish consumption advisories. Ecotoxicology 21(7):1878-1888.

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.

Lepak, J. M., K. D. Kinzli, E. R. Fetherman, W. M. Pate, A. G. Hansen, E. I. Gardunio, C. N. Cathcart, W. L. Stacy, Z. E. Underwood, M. M. Brandt, C. M. Myrick, and B. M. Johnson. 2012b. Manipulation of growth to reduce sport fish mercury concentrations on a whole-lake scale. Canadian Journal of Fisheries and Aquatic Sciences 69(1):122-135.

RESEARCH PRIORITY: **Food webs and predator-prey interactions:** Rainbow Smelt *Osmerus mordax* – Walleye interactions in Horsetooth Reservoir.

OBJECTIVES

To determine if Walleye recruitment failure in Horsetooth Reservoir could be linked to Rainbow Smelt predation on larval Walleye, and to prepare and submit a manuscript with our findings.

PUBLICATION

Lepak, J. M., **A. G. Hansen**, E. T. Cristan, D. Williams, and W. M. Pate. 2023. Rainbow Smelt (*Osmerus mordax*) influence on Walleye (*Sander vitreus*) recruitment decline: mtDNA evidence supporting the predation hypothesis. Journal of Fish Biology. https://doi.org/10.1111/jfb.15523.

BACKGROUND

Rainbow Smelt have been introduced widely in North America, generally to provide forage for other fishes (Evans and Loftus 1987; Mercado-Silva et al. 2006). These introductions have increased growth in a variety of sport fish including Atlantic Salmon *Salmo salar*, Lake Trout, Walleye and other species (Havey 1973; Evans and Loftus 1987; Jones et al. 1994). However, many Rainbow Smelt introductions have been linked with the collapse of fish populations and other undesirable food web shifts (Mercado-Silva et al. 2007), and modeling exercises indicate Rainbow Smelt can dominate invaded systems (Roth et al. 2010). For example, declines in Walleye recruitment and/or abundance have been associated with multiple different introductions of Rainbow Smelt (Schneider and Leach 1977, Johnson and Goettl 1999; Mercado-Silva et al. 2007).

Several hypotheses have been suggested for observed declines in Walleye recruitment following Rainbow Smelt introductions. One primary hypothesis for these observations is that Rainbow Smelt compete for food resources (i.e., zooplankton) with larval Walleye (Evans and Loftus 1987; Johnson and Goettl 1999), and it is known that small Walleye and Rainbow Smelt consume zooplankton. A competing (but not mutually exclusive) hypothesis is that Rainbow Smelt consume larval Walleye after emergence (Mercado-Silva et al. 2007; Lawson and Carpenter 2014). Although widespread, the mechanism or combination of mechanisms driving these observations have not been definitively characterized.

We focused on the hypothesis that Rainbow Smelt are consuming Walleye offspring (larvae/juveniles). Stomach contents were identified from more than 2,000 Rainbow Smelt collected from Horsetooth Reservoir (Larimer County, CO, USA) where declines in Walleye recruitment have been observed twice when Rainbow Smelt abundance was high (Hansen et al. 2021). Though gut content analysis has been conducted to identify larval fish in Rainbow Smelt stomachs, it can be challenging due to breakdown and fragility of larval fish, and visual inspection has not produced evidence of Rainbow Smelt consumption of Walleye to our knowledge with the exception of a single observation in Lake Champlain (Stritzel Thompson et al. 2011). Thus, we used a genetic approach to test for Walleye mitochondrial DNA in Rainbow

Smelt stomach contents collected in spring 2022 near the inlet of Horsetooth Reservoir, a known Walleye spawning area, and a location where we confirmed the presence of larval Walleye.

MANUSCRIPT ABSTRACT

Rainbow Smelt have been introduced widely, but are associated with declines in Walleye recruitment. A primary hypothesis for these declines is that Rainbow Smelt consume larval Walleye. We confirmed overlapping spatial/temporal distributions of larval Walleye and Rainbow Smelt our study system, and used mtDNA analyses to determine if Rainbow Smelt stomach contents contained Walleye. Approximately 20% of Rainbow Smelt composite stomach samples were considered positive for Walleye consumption. These findings support the predation hypothesis, and have Walleye management/stocking implications.

REFERENCES

Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by Rainbow Smelt *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2)249-266.

Hansen, A. G., J. M. Lepak, E. T. Cristan, W. M. Pate, and C. J. Farrell. 2021. Coldwater lake and reservoir research. Colorado Parks and Wildlife. Annual Report, Fort Collins, CO, USA.

Havey, K. A. 1973. Effects of a smelt introduction on growth of land-locked salmon at Schoodic Lake, Maine. Transactions of the American Fisheries Society 102:392-397.

Johnson, B. M., and J. P. Goettl, Jr. 1999. Food web changes over fourteen years following introduction of Rainbow Smelt into a Colorado reservoir. North American Journal of Fisheries Management 19:629-642.

Jones, M. S., J. P. Goettl, Jr., and S. A. Flickinger. 1994. Changes in Walleye food habits and growth following a Rainbow Smelt introduction. North American Journal of Fisheries Management 14:0409-414.

Lawson, Z. J., and S. R. Carpenter. 2014. A morphometric approach for stocking Walleye fingerlings in lakes invaded by Rainbow Smelt. North American Journal of Fisheries Management 34:998-1002.

Mercado-Silva, N., J. D. Olden, J. T. Maxted, T. R. Hrabik, and M. J. Vander Zanden. 2006. Forecasting the spread of invasive Rainbow Smelt in the Laurentian Great Lakes Region of North America. Conservation Biology 20:1740-1749.

Mercado-Silva, N., G. G. Sass, B. M. Roth, S. Gilbert, and M. J. Vander Zanden. 2007. Impact of Rainbow Smelt (*Osmerus mordax*) invasion on Walleye (*Sander vitreus*) recruitment in Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 64:1543-1550.

Roth, B. M., T.R. Hrabik, C. T. Solomon, N. Mercado-Silva, and J. F. Kitchell. 2010. A simulation of food web interactions leading to Rainbow Smelt *Osmerus mordax* dominance in Sparkling Lake, Wisconsin. Journal of Fish Biology 77(6):1379-1405.

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.

Stritzel Thomson, J. L., D. L. Parrish, S. L. Parker-Stetter, L. G. Rudstam, and P. J. Sullivan 2011. Growth rates of Rainbow Smelt in Lake Champlain: effects of density and diet. Ecology of Freshwater Fishes 20:503-512.

RESEARCH PRIORITY: **Triploid Walleye biology:** Recent publication from completed PhD project in collaboration with Colorado State University.

OBJECTIVES

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

PUBLICATION

Farrell, C. J., **A. G. Hansen**, B. M. Johnson, and C. A. Myrick. *In press*. An evaluation of the relative size, body condition, and survival of triploid Walleye in the wild. North American Journal of Fisheries Management.

BACKGROUND

Triploid fish have been frequently used in aquaculture and for aquatic vegetation control (Allen and Wattendorf 1987; Benfey 1999; Maxime 2008; Piferrer et al. 2009). The primary reason for using triploid fish is that they are presumably reproductively sterile. Sterility confers several advantages, such as reproductive and genetic containment should fish disperse from their desired locale and increased growth efficiency (Benfey 1999; Maxime 2008; Piferrer et al. 2009). Interest in using triploid fish as a recreational fisheries management tool, especially in situations where there is a desire to stock nonnative sport fish, is growing because triploid fish provide a lower-risk stocking option, is one of only a few methods available to reconcile the often conflicting goals of sport fisheries management and native species conservation (Martinez et al. 2009; Budy et al. 2012; Cassinelli et al. 2019), and may deter illegal stocking (Johnson et al. 2009). Colorado has been actively stocking triploid Walleye in select Western Slope waters since as early as 2008 to meet various management objectives. A PhD project through Colorado State University was initiated in 2017 to evaluate the biology of triploid Walleye and better inform stocking and management.

MANUSCRIPT ABSTRACT

Natural dispersal or unauthorized introductions of nonnative predatory sport fish can undermine native species conservation and other fisheries management objectives. The use of reproductively sterile triploid fish may provide a lower-risk stocking option (i.e., genetic and reproductive containment) for diversifying angling opportunities while possibly reducing angler motivation to illegally transplant fish. Management interest in triploid Walleye is growing, and these fish are currently stocked by several fisheries agencies. Yet, little is known about the post-stocking growth, body condition, and survival of triploid Walleye; information that is important for calibrating expectations and guiding policy regarding their use. We compared the age-specific size, body condition, and survival of subadult (i.e., ages 0–3) triploid Walleyes to normal diploid conspecifics in two eastern Colorado reservoirs. Paired stockings of triploid and diploid Walleyes occurred over 3 years. Both fry and fingerlings were stocked each year.

Triploids were generally smaller in length (6.6% on average) and weight (20.6%) compared to diploids across all age-classes. Despite being smaller, triploids had similar body condition relative to diploids. On average, the survival of triploids from spring stocking to their first fall was 6.3x lower than that of diploids, but no differences in survival were observed beyond this early life stage. This pattern was consistent across cohorts and reservoirs. This work provides a foundation for future studies designed to clarify patterns of survival from spring to first fall by accounting for size-at-stocking and natural-origin fish, and those planned to assess the post-stocking performance of triploid Walleyes independent of diploids.

REFERENCES

Allen, S. K., and R. J. Wattendorf. 1987. Triploid Grass Carp: status and management implications. Fisheries 12(4):20-24.

Benfey, T. J. 1999. The physiology and behavior of triploid fishes. Reviews in Fisheries Science 7(1):39-67.

Budy, P., G. P. Thiede, A. Dean, D. Olsen, and G. Rowley. 2012. A comparative and experimental evaluation of performance of stocked diploid and triploid Brook Trout. North American Journal of Fisheries Management 32(6):1211-1224.

Cassinelli, J. D., K. A. Meyer, M. K. Koenig, N. V. Vu, and M. R. Campbell. 2019. Performance of diploid and triploid Westslope Cutthroat Trout fry stocked into Idaho alpine lakes. North American Journal of Fisheries Management 39(1):112-123.

Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? Fisheries 34(8):389-394.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western Lake Trout woes. Fisheries 34(9):424-442.

Maxime, V. 2008. The physiology of triploid fish: current knowledge and comparisons with diploid fish. Fish and Fisheries 9(1):67-78.

Piferrer, F., A. Beaumont, J.-C. Falguière, M. Flajšhans, P. Haffray, and L. Colombo. 2009. Polyploid fish and shellfish: production, biology and applications to aquaculture for performance improvement and genetic containment. Aquaculture 293(3-4):125-156.

RESEARCH PRIORITY: **Triploid Walleye stocking procedures:** Exploring the risks of imperfect triploid Walleye stocking in Western Slope waters of Colorado.

OBJECTIVES

Construct a simulation model to evaluate the risks associated with imperfect triploid Walleye stocking. Use the model to quantify the probability of jump-starting a new feral population while stocking fish with triploidy induction rates <100% and under different natural reproduction and reproductive interference scenarios.

PUBLICATION

Hansen, **A. G.**, C. J. Farrell, and B. M. Johnson. 2023. Simulated effects of imperfect sterile sport fish stocking on persistence of fertile fish in new exploited populations. North American Journal of Fisheries Management 43:908-934 (**Published as a Feature Article**).

BACKGROUND

Stocking sterile fish or fish with chromosomal modifications is a common fisheries management practice. Sterile fish are used for aquatic vegetation control (Allen and Wattendorf 1987) and biocontrol of undesirable or overabundant prey fishes, while diversifying sport fisheries (Lepak et al. 2012; Winters et al. 2017; Hansen et al. 2022). Sterile fish can also enhance sport fisheries where preserving the genetic integrity of wild congeners is important (Kozfkay et al. 2006; Koch et al. 2018). Male fish with chromosomal abnormalities, such as sterile triploids—which develop testes that produce ineffective gametes in most species (Warrillow et al. 1997; Tiwary et al. 2004; Piferrer et al. 2009; Benfey 2011)—or “supermales” (i.e., YY fish), could limit unwanted feral populations by interfering with reproduction (Thresher et al. 2014; Schill et al. 2017; Teem et al. 2020), which represents a growing area of research.

In some regions with few native sport fish but strong angler desire for nonnative piscivorous species, sterile fish are being explored as a lower-risk management option. In such settings, conflicts can arise resulting in actions like illegal stocking (Johnson et al. 2009) that undermine competing management objectives related to native fish protection (Tyus and Saunders 2000; Wolff et al. 2012) or existing sport fisheries (Hickley and Chare 2004; Eby et al. 2006; Johnson et al. 2017). The upper Colorado River basin is at the forefront of these issues. One proposed strategy is sterile predator stocking to provide new fisheries in strategic locations, while maintaining reproductive containment to limit interference with other objectives. Given the socioecological complexity of such stocking decisions, managers need objective information to guide discussions with stakeholders and inform policy. The purpose of this work was to provide managers in Colorado objective information for evaluating triploid (sterile) Walleye stocking procedures.

MANUSCRIPT ABSTRACT

Objective: Sterile fish are used for multiple purposes, including enhancing sport fisheries where

reproduction is not wanted. In some regions with few native sport fish, but strong angler desire for nonnative piscivorous species, establishing new fisheries using sterile predators is being explored as a management option. In this context, objective information is needed to guide discussions with stakeholders and inform policy.

Methods: Artificial induction of triploidy is commonly used to produce sterile predators, but the process is rarely 100% effective. Thus, starting a new triploid fishery would require stocking fish with imperfect induction, which carries the risk of jump-starting a feral population if stocked diploids survive to maturity and become self-sustaining. We developed a joint stochastic age structured model to explore the potential consequences of stocking triploid Walleye with imperfect induction into locations devoid of diploids to inform stocking decisions.

Result: Model simulations demonstrated that a high induction rate (≥95%) for triploid fingerling stocking combined with multiple simultaneous constraints on natural reproduction were required to minimize the probability of diploid Walleye persistence or to maintain the abundance of natural-origin fish near or below expectations from stocking alone. Reproductive interference from triploid males could suppress the population expansion of diploids under some circumstances. Above patterns were also contingent on maintaining a relatively high annual mortality rate (>50%)—reflective of exploited populations—on age-classes of Walleye particularly vulnerable to catch and harvest.

Conclusion: Our modeling framework provides decision makers objective information to weigh stocking options and guide discussions. A better understanding of the recruitment and exploitation dynamics of nonnative Walleye populations and the poststocking performance and behavior of triploid Walleye would help refine models and expectations.

REFERENCES

Allen, S. K., and R. J. Wattendorf. 1987. Triploid Grass Carp: status and management implications. Fisheries 12:20-24.

Benfey, T. J. 2011. Physiology of triploid fish. In: Farrell, A. P. (Ed.), Encyclopedia of fish physiology: from genome to environment, vol. 3. Academic Press, San Diego, pp. 2009–2015.

Eby, L. A., W. John Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology and Evolution 21:576-584.

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

Hickley, P., and S. Chare. 2004. Fisheries for non-native species in England and Wales: angling or the environment? Fisheries Management and Ecology 11:203-212.

Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? Fisheries 34:389–394.

Johnson, C. F., B. M. Johnson, T. E. Neebling, and J. C. Burckhardt. 2017. Walleye introduction eliminates predation refuge for adfluvial Cutthroat Trout and Rainbow Trout. Transactions of the American Fisheries Society 146:252-267.

Koch, J., C. Steffen, J. Goeckler, R. Marteney, J. Jagels, and B. Brown. 2018. Comparison of diploid and triploid saugeye recruitment, growth, and condition in Kansas impoundments. North American Journal of Fisheries Management 38:446–453.

Kozfkay, J. R., J. C. Dillon, and D. J. Schill. 2006. Routine use of sterile fish in salmonid sport fisheries: are we there yet? Fisheries 31:392-401.

Lepak, J. M., C. N. Cathcart, and W. L. Stacy. 2012. Tiger muskellunge predation on stocked salmonids intended for recreational fisheries. Lake and Reservoir Management 30:250-257.

Piferrer, F., A. Beaumont, J. C. Falguière, M. Flajšhans, P. Haffray, and L. Colombo. 2009. Polyploid fish and shellfish: production, biology and applications to aquaculture for performance improvement and genetic containment. Aquaculture 293:125–156.

Schill, D. J., K. A. Meyer, and M. J. Hansen. 2017. Simulated effects of YY-male stocking and manual suppression for eradicating nonnative Brook Trout populations. North American Journal of Fisheries Management 37:1054-1066.

Teem, J. L., L. Alphey, S. Descamps, M. P. Edgington, O. Edwards, N. Gemmell, T. Harvey-Samuel, R. L. Melnick, K. P. Oh, A. J. Piaggio, J. R. Saah, D. Schill, P. Thomas, T. Smith, and A. Roberts. Genetic biocontrol for invasive species. Frontiers in Bioengineering and Biotechnology 8:452.

Thresher, R. E., K. Hayes, N. J. Bax, J. Teem, T. J. Benfey, and F. Gould. 2014. Genetic control of invasive fish: technological options and its role in integrated pest management. Biological Invasions 16:1201–1216.

Tiwary, B. K., R. Kirubagaran, and A. K. Ray. 2004. The biology of triploid fish. Reviews in Fish Biology and Fisheries 14:391-402.

Tyus, H. M., and J. F. Saunders. 2000. Nonnative fish control and endangered fish recovery: lessons from the Colorado River. Fisheries 25:17–24.

Warrillow, J. A., D. C. Josephson, W. D. Youngs, and C. C. Krueger. 1997. Differences in sexual maturity and fall emigration between diploid and triploid Brook Trout (*Salvelinus fontinalis*) in an Adirondack lake. Canadian Journal of Fisheries and Aquatic Sciences 54:1808–1812.

Winters, L. K., P. Budy, and G. P. Thiede. 2017. Earning their stripes: the potential of tiger trout and other salmonids as biological controls of forage fishes in a western reservoir. North American Journal of Fisheries Management 37:380-394.

Wolff, B. A., B. M. Johnson, A. R. Breton, P. J. Martinez, and D. L. Winkelman. 2012. Origins of invasive piscivores determined from the strontium isotope ratio ($^{87}Sr/^{86}Sr$) of otoliths. Canadian Journal of Fisheries and Aquatic Sciences 69:724-739.

RESEARCH COMMUNICATION & TECHNICAL ASSISTANCE

Reporting period: December 2022 – November 2023.

Peer-Reviewed Publications

- Beauchamp, D. A., **A. G. Hansen**, and D. Parrish. *In press.* 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.

- Chao Guo, Shiqi Li, Jie Ke, Chuansong Liao, **A. G. Hansen**, E. Jeppesen, Tanglin Zhang, Wei Li, and Jiashou Liu. 2023. The feeding habits of small-bodied fishes mediate the strength of top-down effects on plankton and water quality in shallow subtropical lakes. Water Research 233:119705.

- Farrell, C. J., **A. G. Hansen**, M. M. Brandt, C. M. Myrick, and B. M. Johnson. *In press*. An evaluation of the relative size, body condition, and survival of triploid Walleye in the wild. North American Journal of Fisheries Management.

- **Hansen, A. G.**, C. J. Farrell, and B. M. Johnson. 2023. Simulated effects of imperfect sterile sport fish stocking on persistence of fertile fish in new exploited populations. North American Journal of Fisheries Management 43:908-934 (**Feature Article**).

- **Hansen, A. G.**, A. K. McCoy, G. P. Thiede, and D. A. Beauchamp. 2023. Pelagic food web interactions in a large invaded ecosystem: implications for reintroducing a native top predator. Ecology of Freshwater Fish 32:552-570.

- **Hansen, A. G.**, M. W. Miller, E. T. Cristan, C. J. Farrell, P. Winkle, M. M. Brandt, K. D. Battige, and **J. M. Lepak**. 2023. Gill net catchability of Walleye (*Sander vitreus*): are provincial standards suitable for estimating adult density outside the region? Fisheries Research 266:106800.

- **Lepak, J. M.**, **A. G. Hansen**, E. T. Cristan, D. Williams, and W. M. Pate. 2023. Rainbow Smelt (*Osmerus mordax*) influence on Walleye (*Sander vitreus*) recruitment decline: mtDNA evidence supporting the predation hypothesis. Journal of Fish Biology. https://doi.org/10.1111/jfb.15523.

- **Lepak, J. M.**, B. A. Wolff, B. M. Johnson, M. B. Hooten, and **A. G. Hansen**. 2023. Predicting sport fish mercury contamination in heavily managed reservoirs: implications for human and ecological health. PLoS ONE 18(8):e0285890.

Manuscripts Submitted for Publication

- **Hansen, A. G.**, **J. M. Lepak**, E. I. Gardunio, and T. Eyre. *In review.* Controlling socially-valued, but ecologically-detrimental fish: evaluating harvest incentives for suppressing an invasive freshwater predator. Fisheries Management and Ecology.

External Presentations

- **Lepak, J. M.**, D. Winkelman, **A. G. Hansen**, J. Ewert, and T. Eyre. Sterile tiger muskellunge (*Esox lucius x E. masquinongy*) as undesirable fish species control agents. Colorado State University Cooperative Fish and Wildlife Research Unit annual review. May 3, 2023. Fort Collins, CO.

- **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. February 3, 2023 (virtual).

- **Lepak, J. M.** Characterizing lake and reservoir ecosystems: simple and complex models. Guest lecture for Jennifer Lee. Front Range Community College. April 27, 2023. Fort Collins, CO.

Internal Presentations

- **Lepak, J. M.**, D. Winkelman, **A. G. Hansen**, J. Ewert, and T. Eyre. Sterile tiger muskellunge (*Esox lucius x E. masquinongy*) as undesirable fish species control agents. CPW Coldwater Reservoir Management Meeting. February 8th, 2023 (virtual).

Other Research Communication & Technical Assistance

- Anonymous peer reviewer for: Biology (1 ms), Environmental Biology of Fishes (1 ms); Fishes (2 ms); Hydrobiologia (1 ms); Movement Ecology (1 ms).

- Provided analytical assistance to Mandi Brandt regarding CPW versus AFS gill netting comparisons.

- Provided size-at-age information from smallmouth bass in Colorado to Anthony Rodger with Oklahoma Department of Wildlife Conservation for manuscript evaluating broad-scale growth patterns.

- Provided otolith processing assistance to John Woodling and Eric Gardunio.

- Provided baseline information culminating in the publication:

  Lauber, T. B., **J. M. Lepak**, N. A. Connelly, B. Schroeder, R. C. Stedman, B. A. Knuth, and S. L. Furgal. 2022. Stakeholder and manager responses to the Lake Huron Chinook Salmon fishery collapse: Informing future decision making. Center for Conservation Social Sciences Publ. Series 22-3. Dept. of Nat. Resources and the Environ., Coll. Agric. and Life Sci., Cornell Univ., Ithaca, NY. 54 pp.

- Provided expertise on species-specific sport fish mercury bioaccumulation to CDPHE personnel (Meghan Williams and Aki Suzuki).