5-2024

Informing Control Efforts for a Prolific Invasive Species: Characterizing Common Carp Spatio-Temporal Distribution and Evaluating the Impacts of Gear Selectivity in Utah Lake

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Recommended Citation

Fadlovich, Rae, "Informing Control Efforts for a Prolific Invasive Species: Characterizing Common Carp Spatio-Temporal Distribution and Evaluating the Impacts of Gear Selectivity in Utah Lake" (2024). *All Graduate Theses and Dissertations, Fall 2023 to Present*. 153.
https://digitalcommons.usu.edu/etd2023/153

INFORMING CONTROL EFFORTS FOR A PROLIFIC INVASIVE SPECIES: CHARACTERIZING COMMON CARP SPATIO-TEMPORAL DISTRIBUTION AND EVALUATING THE IMPACTS OF GEAR SELECTIVITY IN UTAH LAKE

by

Rae Fadlovich

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Timothy E. Walsworth, Ph.D. Major Professor	Sarah E. Null, Ph.D. Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2024

ABSTRACT

Informing Control Efforts for a Prolific Invasive Species: Characterizing Common Carp Spatio-Temporal Distribution and Evaluating the Impacts of Gear Selectivity in Utah Lake

by

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Utah State University, 2024

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Control programs that aim to mitigate the consequences of invasive species are often challenged by highly fecund invaders and selective removal gears. Selectivity, the relative impact of harvest on different size classes, can contribute to population recovery when younger fish are not effectively targeted. In Utah Lake, the location of one of the world's largest freshwater vertebrate species control programs, managers have been attempting to control common carp (*Cyprinus carpio*, hereafter "carp") since 2009 but efforts have been hindered by the use of selective fishing gears. I conducted a lake-wide field study to gain insights into the spatio-temporal distribution of juvenile and small adult carp and to identify alternative gears that can be incorporated in control efforts. I used a hurdle generalized linear mixed effects model assuming a negative binomial error structure to evaluate catch of juvenile, small adult, and all ages of carp, identifying strong temporal trends across years, with carp presence in a sample being 125 to 270 times more likely in 2023 than 2021. While the highly variable nature of Utah Lake impacted my study and additional sampling might provide further insights, it is important to assess which age classes confer the most benefit for population control when captured. To do this, I used a simulation framework that integrates age-based gear selectivity and the widely implemented fisheries metric of maximum sustainable yield (MSY) to evaluate the effect of improving selectivity. I found that improving selectivity on younger, but mature, age classes could achieve the control program's biomass target with only 2.5 times maximum historic effort, while further increasing juvenile selectivity conferred minimal additional benefit. Historic fishing effort was below that required to generate MSY regardless of selectivity, suggesting the control program would be harvesting at a sustainable rate even if gear selectivity were improved and effort increased. Controlling highly fecund invasive species becomes much more feasible if an approach that targets all adult age classes can be identified. Incorporating sustainable harvest metrics into simulation models of invasive species populations provides a framework for evaluating a harvest control program's ability to overcome density-dependent processes and achieve management objectives.

(97 Pages)

PUBLIC ABSTRACT

Informing Control Efforts for A Prolific Invasive Species: Characterizing Common Carp Spatio-Temporal Distribution and Evaluating the Impacts of Gear Selectivity in Utah Lake

Rae Fadlovich

Management programs that aim to reduce the consequences of invasive species are often challenged by populations that can rapidly recover from removal efforts. Selectivity, the relative impact of harvest on different size classes, can contribute to population recovery when younger fish are not effectively targeted. In Utah Lake, the location of one of the world's largest freshwater fish control programs, managers have been attempting to control the common carp (*Cyprinus carpio*, hereafter "carp") population since 2009 but efforts have been hindered by the use of selective fishing gears. I conducted a lake-wide field study to gain insights into the distribution of juvenile and small adult carp in time and space and to identify fishing gears that can be incorporated in control efforts. I evaluated factors influencing the presence and abundance of juvenile, small adult, and all ages of carp in survey samples, and identified strong temporal trends across years, with carp catch being 125 to 270 times more likely in 2023 than 2021. While the highly variable nature of Utah Lake impacted my study and additional sampling might provide further insights, it is important to assess which age classes are the most critical to capture. To do this, I used a simulation framework that integrates age-based gear selectivity and the widely implemented commercial fisheries metric of maximum sustainable yield (MSY) to evaluate the effect of improving selectivity among younger carp. I found that improving selectivity on younger, but mature, age classes achieved the control program’s biomass target with only 2.5 times maximum historic effort, while further improving juvenile selectivity had minimal benefit. The historic level of fishing effort was below that required to achieve MSY regardless of selectivity scenario, suggesting the control program would be harvesting at a sustainable rate even if gear selectivity were improved. Controlling invasive species becomes much more feasible if an approach that targets all adult age classes can be identified and incorporating sustainable harvest metrics into simulation models of invasive species populations provides a framework for evaluating a harvest control program’s ability to achieve management objectives.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Timothy E. Walsworth, for giving me the opportunity to conduct this research. I am very grateful that you encouraged me to pursue my interests throughout this project. Thanks to your support and mentorship, I will start a dream Ph.D. position in the fall. It has been a wonderful opportunity to be a part of the Quantitative Fisheries and Aquatic Ecology Lab. I am especially thankful for Kevin Landom, who has provided endless Utah Lake expertise and guidance throughout this project. This work was funded by the June Sucker Recovery Implementation Program (JSRIP), and I would like to thank them for making this research possible and providing feedback along the way.

I would also like to thank the many people at USU who have supported my research. Thank you to my committee members, Dr. Sarah Null and Dr. Sarah Klain, for your feedback and support. Thanks to the Fish Ecology Lab for your camaraderie, and especially to Dr. Phaedra Budy and Gary Thiede for your mentorship. I am also very grateful to have had the support of Erline Vendredi, Thad Nicholls, and Brian Bailey.

I am also thankful for the many technicians who have assisted with my research and helped me grow as a mentor. Thanks to Austin Garner, Autumn Zierenberg, Gabe McLaughlin, Paige Sargeant, and Tom Doolittle for your help on Utah Lake. I am also grateful for Abby Lane, Brinley Olsen, Julia Sluiter, and Quinn Olpin for their support in the lab and during lab meetings. Oh, and thank you to Cristina Chirvasa for being a great technician, researcher, and friend.

I would also like to thank the friends that spent time on the lake with me. Thanks to Skylar Rousseau and Ben Miller for taking time out of their own field schedules to experience the beauty of Utah Lake. Thank you to Chloe Lyles for your support on and off the lake. A big thank you to Kadie Heinle, not only for your help in the field but for being a role model and friend. And of course, a big thank you to Eryn Turney for being a fantastic cat sitter, fieldwork assistant, defense cheerleader, and friend. Speaking of cats, a big thank you to my cat, Bufo.

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CHAPTER I

INTRODUCTION

Invasive species are one of the greatest threats to global biodiversity, posing a threat to native species, communities, and ecosystems (Clavero & García-Berthou, 2005; Doherty et al., 2016; Reid et al., 2005; Simberloff, 2001). Invasive species alter ecosystems' physical features, nutrient cycling, and plant and animal communities, and lead to losses in crops, fisheries, forestry, and grazing capacity (Early et al., 2016; Gallardo et al., 2015; Mack et al., 2000; Pimentel et al., 2005). Invasive species management ranges from measures to curb introductions (Mack et al., 2000), control population growth and spread (Gaeta et al., 2015; Hansen et al., 2013; Rytwinski et al., 2018; Walsworth et al., 2020), or fully eradicate a population (Gaeta et al., 2012; Rytwinski et al., 2018; Yick et al., 2021). The scale of invasion, intensity of control methods, and the ability to locate and remove invaders affect the management project's cost, duration, and likelihood of success, making the control of species in larger ecosystems more difficult and costly (Myers et al., 2000; Rejmánek & Pitcairn, 2002; Rytwinski et al., 2018; Simberloff, 2003). Long-term suppression of invasive species is often seen as more feasible than full eradication, but these control efforts often require a combination of control tactics and continual suppression for success (Baker et al., 2017; Green & Grosholz, 2021; Simberloff, 2003).

Introduced fish can alter food web structure (Eby et al., 2006; Flecker & Townsend, 1994), contribute to the extirpation and extinction of native species (Kaufman, 1992; Miller et al., 1989; Witte et al., 1992), lead to biodiversity loss (Light & Marchetti, 2007; Ricciardi & MacIsaac, 2010), and produce negative economic impacts on commercial fisheries (Mills et al., 1993; Pimentel et al., 2005). These negative effects arise from several processes including the spread of pathogens, predation, parasitism, competition, alteration of habitat structure, and hybridization with native species (Cucherousset & Olden, 2011). Because of the negative effects invasive species pose to freshwater ecosystems, they are frequently the target of control efforts (Rytwinski et al., 2018). While control efforts are often seen as more feasible than complete eradication, much of the information about these efforts is in grey literature (e.g., SWCA, 2005, 2006) while eradication efforts are likely disproportionately represented in peer-reviewed literature (e.g. Rytwinski et al., 2018).

Common carp (*Cyprinus carpio*; *hereafter* "carp"), a cyprinid native to Eurasia that were frequently introduced to new systems as a food source, have become widely established and are one of the most prevalent and damaging invasive species in the world (Hicks & Ling, 2015; Lowe et al., 2000; Weber & Brown, 2009). Carp are benthic omnivores known to reduce water quality, uproot aquatic macrophytes, increase turbidity, enrich nutrient loads, and reduce invertebrate biomass (Bajer et al., 2012; Bajer & Sorensen, 2015; Matsuzaki et al., 2009; Zambrano & Hinojosa, 1999). As such, carp are one of the most common freshwater fishes subject to documented removal efforts (Rytwinski et al., 2018). Like other invasive fishes, carp have proven especially difficult to remove in large freshwater systems (Walsworth et al., 2020; Weber et al., 2016) and a review of common carp removal efforts found evidence of only two successful carp eradications: one in Minnesota (lake surface area of 0.1 km^2) and one in Tasmania (23 km^2) (Bivens et al. 2021).

Carp were introduced to Utah Lake (380 km^2), a large intermountain lake in Utah County, Utah, in the 1880s as a food source to supplement the native trout fishery (Heckmann et al., 1981). Ongoing overharvest, species introductions, water development, and nutrient loading led to many changes in the lake, and by the early 2000s, the carp population made up over 90% of Utah Lake fish biomass (SWCA, 2002) and led to increased turbidity, altered food web dynamics, and the loss of aquatic vegetation (King et al., 2024). Carp also pose a threat to the endemic June sucker (*Chasmistes liorus*), which was listed as an endangered species in 1986 and down-listed to threatened in 2021 (USFWS, 2021). The June sucker down-listing was attributed to a substantial increase in spawning population resulting from ongoing hatchery stocking efforts and enhanced habitat quality, due in part to ongoing carp removal.

To mitigate the negative effects of carp on Utah Lake habitat and June sucker recruitment, managers began targeted removals of carp in 2009, setting a biomass reduction goal of 75% (SWCA, 2005, 2006). These efforts have removed over 13,000 tons of carp through 2023, making it one of the largest freshwater fish removal efforts in the world (Walsworth et al., 2020, 2023). Despite the impressive biomass of carp removed, catch is dominated by the oldest and largest individuals (Walsworth et al., 2020, 2023), allowing for compensatory recruitment of juveniles. An age-structured, integrated population model of Utah Lake carp found that while biomass reduction targets likely were close to being met in 2017, carp levels have since increased and the likelihood of maintaining the carp reduction goal in the long-term is unlikely with current removal activities (Walsworth et al., 2020, 2023). Mechanical removal gears, such as the seine nets used in the Utah Lake carp control efforts, are size-selective for larger individuals and typically less effective at targeting small, juvenile fish (Millar & Fryer, 1999).

In this thesis, I seek to improve our understanding of the spatio-temporal distribution of juvenile and smaller adult carp in Utah Lake and to evaluate the impact of size- or age-selectivity on the efficacy of invasive species control programs. Selectivity is the relative impact of harvest on different size- or age-classes and has long been discussed in commercial fisheries because of the impact it can have on sustainable harvest (Beverton & Holt, 1957; Vasilakopoulos et al., 2016; Wileman et al., 1996). Selectivity comprises both gear selectivity, the size of fish that can physically be captured by a gear, and population selectivity, the proportion of a given size of the population that is impacted by harvest (Millar & Fryer, 1999). Population selectivity therefore is not only impacted by the gear characteristics, but the spatio-temporal distribution of both the fish and the harvest (Scott & Sampson, 2011).

In Chapter II, I conduct a field study to 1) evaluate alternative mechanical removal gears and 2) determine the spatio-temporal distribution of juvenile and small adult carp in Utah Lake. Between August of 2021 and June of 2023, I conducted a lake-wide field study with multiple alternative mechanical removal gears including mini trap nets (hereafter "trap nets"), gillnets, boat-pulled beach seines, hand-pulled beach seines, and minnow traps deployed at 16 sites around the perimeter of the lake. Trap nets (mini-trap or mini-fyke nets) were the most effective at capturing juvenile and small adult carp, although their performance was not sufficient to recommend inclusion in the carp control efforts. I then use a hurdle mixed effects model to analyze the spatio-temporal distribution of carp catch in the trap nets. I found that juvenile and small adult carp were more likely to be captured later in the spawning season and in high water years and were caught in higher numbers in the middle of spawning season and when the population was larger. Carp of all ages were less likely to be found at rocky sites, which is congruent with current commercial fisheries avoidance of rocky sites. Results from this field study are limited in part due to the low catch of smaller carp and dynamic lake conditions. While more extensive surveys may better elucidate trends, targeting juvenile carp may not be the only strategy for effective control.

In Chapter III, I develop a simulation framework that incorporates age-based gear selectivity and the widely implemented fisheries metric of maximum sustainable yield (MSY) to evaluate the effect of improving gear selectivity among cryptic age classes for invasive species population control. While it has previously been suggested that successfully controlling invasive common carp requires successfully targeting all age classes, doing so can be costly and difficult to achieve (Weber et al., 2016; Yick et al., 2021). Results from my simulation suggest that the likelihood of successful control significantly increases if all adult age classes are well selected for, but there is little additional benefit realized from improving selectivity on juvenile ages. I find that historic levels of carp fishing effort in Utah Lake are well below MSY regardless of selectivity scenario, suggesting the control program would be harvesting sustainably even if gear selectivity were improved. These results can inform managers in Utah Lake and elsewhere of the life stages that are most beneficial to target, can inform the design of future field studies, and provide a framework for evaluating the long-term implications of invasive species harvest.

In Chapter IV, I synthesize the findings of my two research chapters into general conclusions regarding the control of highly fecund invasive species and the resources necessary to overcome their density-dependent population responses. Though much work has been done regarding the control of invasive common carp (e.g. Sorensen & Bajer, 2020; Weber et al., 2016; Yick et al., 2021) and other invasive species (Shyu et al., 2013; Zipkin et al., 2009), managers still struggle to overcome the density-dependent population responses to harvest especially when highly age-selective gears are used (Walsworth et al., 2020; Weber et al., 2011). Identifying gears and fishing methods to improve selectivity are of urgent need to managers. When removal methods cannot be easily identified, simulation models are a useful tool for rapidly evaluating a large number of management actions (van Poorten et al., 2018; Vasilakopoulos et al., 2020; Weber et al., 2011). Integrating common commercial fisheries metrics into a simulation framework allows me to increase our understanding of the implications of gear selectivity in invasive species management. By combining fisheries management theory, simulation modeling, and field-based insights, I am able to evaluate the likelihood of control success for Utah Lake's common carp control program and address knowledge gaps that many invasive species management programs.

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CHAPTER II

EXPLORING THE SPATIO-TEMPORAL DISTRIBUTION OF CRYPTIC AGE CLASSES OF A PROLIFIC INVADER IN A LARGE SHALLOW LAKE

Abstract

Managers in Utah Lake have been removing common carp, one of the world's worst invasive species, since 2009 but their efforts have been hindered by the use of removal gears that do not effectively capture cryptic juvenile or small adult carp and result in compensatory population dynamics. We conducted a lake-wide field study with multiple alternative mechanical removal gears to gain insights into the spatio-temporal distribution of juvenile and small adult carp and to identify alternative gears that can be incorporated in control efforts. We then used a hurdle generalized linear mixed effects model assuming a negative binomial error structure to evaluate catch of juvenile, small adult, and all ages of carp. We identified strong temporal trends across years, with a 125 to 270 times greater likelihood of catching carp in 2023 than 2021. We found the western shoreline was negatively associated with catch probabilities for all ages of carp compared to the eastern shoreline and that rocky substrate negatively influenced catch of all age classes. Even though the highly variable nature of Utah Lake impacted our study, we find effects that are consistent with other sampling programs and previous work in Utah Lake while still providing novel insights regarding the optimal seasonality to target juvenile and small adult carp in our system. This study and the insights it provides are an important piece of implementing science driven management in a large invasive species control program for one of the world's worst invasive species.

Introduction

Invasive species are one of the largest threats to global biodiversity, posing a threat to native species, communities, and ecosystems (Clavero & García-Berthou, 2005; Early et al., 2016; Reid et al., 2005; Simberloff, 2001; Vitousek et al., 1997). Globally, managers aim to mitigate these impacts via eradication and control efforts (Britton et al., 2011; Doherty et al., 2016; Simberloff, 2001). In invasive fisheries management, the most common method of control is mechanical removal (Rytwinski et al., 2018) though these efforts are often challenged by size-selective removal gears. Gears that are too large to physically capture younger individuals or that do not effectively sample juvenile associated habitats can limit a control program's ability to overcome compensatory population dynamics (Walsworth et al., 2020; Weber et al., 2016). Ontogenetic shifts in resource use, where an organism's dietary preferences and habitat use change as they grow, are nearly universal in fish (Werner & Gilliam, 1984; Werner et al., 1977) and can make an individual more or less vulnerable to capture across different life and environmental conditions (Snover, 2008). Identifying the spatio-temporal habitat associations of various life-stages is a critical step in successful control as multiple complimentary management approaches that adapt to changing conditions are often necessary for successful invasive species management (Baker et al., 2017; Yick et al., 2021).

Common carp (*Cyprinus carpio*; *hereafter* "carp"), a cyprinid native to Eurasia, are one of the most prevalent and damaging invasive species in the world (Hicks & Ling, 2015; Lowe et al., 2000; Weber & Brown, 2009) and are known to reduce habitat availability and water quality (Bajer & Sorensen, 2015; Matsuzaki et al., 2009). Carp are one of the most common freshwater fishes subject to documented removal efforts (Rytwinski et al., 2018; Yick et al., 2021) and have proven especially difficult to remove in large freshwater systems (Weber et al., 2016; Walsworth et al., 2020). Carp are highly fecund, and removal efforts are often challenged by compensatory recruitment following removal with size-selective fishing gears (Walsworth et al., 2020; Yick et al., 2021). Like many fish, carp have a complex life history and occupy different habitats during spawning, foraging, and overwintering (Hicks & Ling, 2015). Young-of-year carp are typically found in shallow water with submerged or inundated emergent macrophytes or woody debris (Edwards & Twomey, 1982; Lechelt et al., 2017; Penne and Pierce, 2008) and leave the nursery habitat between ages zero and two (Weber & Brown, 2013).

Carp were introduced to Utah Lake, a large intermountain lake in Utah County, Utah, in the 1880s as a food source (Heckmann et al., 1981) and made up over 90% of Utah Lake fish biomass by the early 2000s (SWCA, 2002). Carp in Utah Lake increase turbidity, alter food web dynamics, reduce aquatic vegetation (King et al., 2024), and pose a threat to the endemic June sucker (*Chasmistes liorus*), which was listed as an endangered species in 1986 and down-listed to threatened in 2021 (USFWS, 2021). To mitigate these negative effects, managers began targeted removals of carp in 2009, aiming to reduce carp biomass by 75% (SWCA, 2005, 2006). Removal efforts have been conducted by commercial fishers using large beach seines that typically have a 1½-inch mesh. Despite extensive removal efforts, catch is dominated by the oldest and largest individuals, allowing younger and smaller individuals to reproduce before they are removed (Walsworth et al., 2020). An age-structured, integrated population model of Utah Lake carp found that while biomass reduction came close to the target in 2017, carp levels have since increased and the likelihood of maintaining the carp reduction goal in the long-term is unlikely with current removal activities (Walsworth et al., 2020; Walsworth, Wallace, et al., 2023).

Managers can deploy a range of alternative means of physically capturing fish (e.g., gill nets, seines, trap nets, angling; hereafter "gears"), each of which are selective for different sizes of fish and are more or less effective in different habitats. Given the difficulty experienced capturing smaller carp with the 1½ inch mesh commercial seine used in Utah Lake, managers recently conducted surveys using a smaller ¾ inch mesh seine to evaluate effectiveness for smaller size classes of carp. However, gear selectivity analysis found no improvement in selectivity of juvenile or small adult carp with the smaller mesh seine (Fadlovich et al., *Chapter III*). The average carp caught in Utah Lake is over 300cm by one year of age (Walsworth, Wallace, et al., 2023), and thus should be susceptible to capture by either the small mesh or large mesh sizes deployed by the fishery. The large size of carp combined with the fact other species of fish are captured at smaller sizes with this same gear (Fadlovich et al., *Chapter III*) suggest differences in spatio-temporal distribution and habitat use contribute to low catch of juvenile and small adult carp, rather than the mesh size simply being too large.

Large cohorts of juvenile carp are observed following high water years with extensive inundated vegetation in Utah Lake, suggesting they use and benefit from this habitat (Walsworth & Landom, 2021). However, carp removal efforts in Utah Lake have historically targeted nearshore unvegetated habitat with large visible congregations of adult carp (Walsworth et al., 2020), in part because large seines are difficult to effectively pull through shoreline, vegetated habitats. Identifying alternative gears that may improve the control program’s ability to target nearshore habitats that are too shallow or vegetated for the effective use of large commercial seines may thus improve program effectiveness. Other programs have had success in controlling invasive fishes by capturing juvenile individuals with the use of multiple gears including gillnets and trap nets (Dauphinais et al., 2018; Yick et al., 2021). However, the effectiveness of these alternative gears can be impacted by many factors including depth, vegetation presence, or lake size (Collins et al., 2017, Diggle et al., 2012; Driver et al., 2005). Gaining insights into alternative gears and targeted habitats given specific management objectives and ecosystem characteristics is an important step in research-based management programs.

Here, I detail a study to inform control efforts for a globally invasive fish in a large, open lake ecosystem by examining the relative effectiveness of multiple physical capture methods for small size classes. I quantify the spatio-temporal distribution of juvenile common carp in Utah Lake, and the performance of alternative mechanical removal gears. Specifically, I address the following questions for Utah Lake:

- How does catch differ between alternative mechanical removal gears?
- Do capture rates of juvenile and small adult carp vary among sampling month and year?
- Do capture rates of juvenile and small adult carp vary among habitat types (i.e., substrate conditions) and shorelines (north, east, south, west)?

Methods

Site description

Utah Lake is a large, shallow lake located in Utah County, Utah, USA. The lake has a surface area of approximately 380 km^2 at full pool and an average depth of 3.2

meters. Its east, north, and northwest shores are highly urbanized, with agriculture, industrial activities, and public lands along the south and west shore. Utah Lake is primarily fed by melting snowpack in the Wasatch Mountains to the east and inter-basin water transfers from the Colorado River Basin. While Utah Lake is a natural lake and a remnant of historic Lake Bonneville, its only outlet, the Jordan River, has been dammed for use as an irrigation supply (King et al., 2024; Walsworth et al., 2020), contributing to large intra-annual water level fluctuations. Additionally, like many water bodies in the intermountain west, Utah Lake has experienced drastically fluctuating lake levels in recent years due to multi-year drought conditions, climate variability, and management actions. When water levels are low, shoreline macrophyte habitat becomes disconnected from the lake (Dillingham, 2022). 2021 and 2022 were part of a multi-year drought with low lake levels while 2023 was an abnormally wet year with much higher lake levels.

Field surveys

We implemented a standardized study design with 16 shoreline sites (Figure 1), representative of the different geographic regions and littoral habitat types in the lake. The standardized study sites were sampled eight times between August 2021 and June 2023 during April, June, August, and October. Sampling corresponded with the start of carp spawning, which usually occurs in late April when the water temperature reaches 18-20 degrees Celsius (Bivens et al., 2021). Gears were first selected via a systematic review of carp removal literature (Bivens et al., 2021) and further refined based on field observations.

We used two primary mechanical removal gears: mini-trap nets (hereafter trap nets) and gillnets at all sites. The trap nets had a 2-foot by 4-foot frame with a single throat, a 25-foot lead, and a ⅛-inch mesh. Trap nets were deployed overnight in strings of three (August 2021) or two (all other months) with the lead of the second net attached to the pot of the front net. Utah Lake's shallow bathymetry and low lake levels prohibited all nets from being set to shore, so we set all nets as close to shore as possible while ensuring the net's throat was fully submerged. We recorded each trap's depth in the water, distance from nearest shoreline, distance to any vegetation if present, and time elapsed between start and end of deployment in minutes. We also deployed two American Fisheries Society-specified monofilament experimental gillnets, a small net measuring 30 feet long by six feet deep with ⅜-inch, ½-inch, and ⅝-inch mesh panels, and a standard experimental gillnet measuring 80-feet long by six-feet deep with mesh ranging from ¾ to 2½-inches. We deployed gillnets in water that was at least one meter deep and as close to shore as possible and removed them 20 minutes after deployment at all sites. While gillnets traditionally have a longer soak time, we limited duration to mitigate impacts to the endemic and threatened June sucker.

We opportunistically used hand seines, boat-deployed seines, minnow traps, and backpack electrofishing at standardized and supplemental sites when conditions allowed. Strings of five wire-mesh minnow traps were set at most sites, as they could be deployed closer to the shore when conditions were too shallow for shore-set trap nets. We used hand-pulled beach seines at sites when conditions were favorable, though dead shoreline vegetation and deep mud limited their effectiveness. We also opportunistically sampled with a larger, boat-pulled beach seine, although low lake levels made it difficult to implement during 2021 and 2022 as boats could not get close enough to shore to enclose fish. We used a Smith-Root backpack electrofishing unit to sample the shoreline alone and in conjunction with beach seines, though high water conductivity severely limited effectiveness so we excluded this method from analysis.

We identified all fish captured to species and recorded lengths and weights from at least the first ten individuals of each species in each net. For carp, we measured length for all individuals and weights for the first 30 carp at each site. To classify the substrate at each site, we collected grab samples every meter from a 10m-by-10m quadrat at each site to identify the percent of sand, mud, and rock present during April 2022. Since muddy habitat dominates the lake, we identified the two sites with the highest percentage of rock and the two sites with the highest percentage of sand to be rock and sand sites respectively. While we recorded the presence of vegetation during each site visit, we did not characterize sites as vegetated or unvegetated since this characteristic was not consistent due to lake level fluctuations.

Environmental data

To determine the influence of environmental drivers on carp catch, we obtained weather, water quality, and lake level data to include in our analysis. Weather data (daily average air temperature, wind speed, wind direction, precipitation, cloud cover, and UV index) was obtained from Visual Crossing (Visual Crossing Corporation, 2023). Water quality data from continuous sampling buoys were provided by Utah Department of Environmental Quality, Lake level estimates were provided by the Bureau of Reclamation and the Central Utah Water Conservancy District in Orem, Utah.

Analysis of catch

To summarize our field surveys, we first analyzed the fish catch data for (1) total catch by species and gear, (2) length frequency and species composition of the top three gear types, and (3) carp catch-per-unit effort (CPUE) by gear type. We considered one trap net, gill net, minnow trap, or one seine haul to be one unit of effort. We then assessed the trap net data for (4) carp catch by age, (5) length frequency relative to other species, and (6) carp catch at each sample site.

To determine the spatio-temporal variation among carp of different ages, we used linear mixed effects models fit to three different age classifications of carp: ‘juvenile’ (age two and below to represent carp that have not yet reached reproductive age in Utah Lake), ‘small’ (age five and below to represent ages not effectively caught with commercial gears), and ‘all ages’ carp caught in each trap net. The age-composition of carp caught was calculated with a probabilistic approach based on length-at-age estimates from a Von Bertalanffy growth curve fit to length-at-age data (ages estimated from the dorsal spines of a subset of carp collected during another monitoring project) and length-frequency data by Walsworth et al. (2020; updated in Walsworth, Wallace, et al., 2023).

For each age class, we first assessed catch with a generalized linear mixed model with a negative binomial distribution:

$$c_i \sim NB\left(u_i, u_i\left(1+\frac{u}{\theta}\right)\right)$$

$$E(c_i|b_i) = u_i$$

$$b_i \sim N(0, \sigma_u^2\ )$$

$$V(c_i|b_i) = u_i\left(1+\frac{u_i}{\theta}\right)$$

$$\log(u_i) = \log(T_i) + x_i'\,\beta + z_i' b_i$$

where c_i is the catch in net i and the mean parameters u_i are related to the predictor variables x_i' and the sample variables z_i' (random effects) through the logarithm link function and θ is the estimated negative binomial overdispersion. x_i' is a vector of predictor variables, β is a vector of estimated parameters, z_i' is a vector of random effects groupings for the random site effect b_i which is assumed to have a multivariate normal distribution where σ_u^2 is the among-site variance in random effects. We included an offset of net soak time, $\log(T_i)$, to account for difference in soak times between nets. We used nbinom2 in the glmmTMB package (Brooks et al., 2017) which assumes a quadratic variance.

We also examined catch with a hurdle negative binomial mixed effects model, where the hurdle model component estimates the probability of whether any carp of the target age were encountered in a net:

$$y_i \sim Bernoulli(p_i)$$

$$logit(p_i) = x_i'\beta + z_i' b_i$$

where y_i is the probability that net *i* has carp of a given age class (while glmmTMB models the hurdle as the probability that net *i* has no carp of a given age, we present the probability of success in our figures as this is most intuitive) and follows a Bernoulli distribution. The logit link is used to connect the random and fixed effects and we allow the composition of x_i' and β to differ from the negative binomial count component. To assess counts for nets that pass the presence/absence hurdle, we used a truncated negative binomial distribution that follows the same parameters as Formula 1., but only considers counts beginning at one (Shonkwiler, 2016).

We assessed five broad categories of predictor variables including temporal effects of year and month, spatial effects of shoreline and substrate, lake level effects, trap positioning effects, and weather effects (Table 1). To standardize the magnitude of continuous effects, we mean centered and scaled all continuous effects (Zuur et al., 2009) and report them in units of standard deviation from the mean size.

We used Akaike's Information Criterion (AIC) to evaluate support for competing models. For the negative binomial models, we identified the best model using a stepped forward and backward selection by stepwise comparing AIC values where each term could be added or removed at each step of the selection process. We fit the hurdle component first since the negative binomial model faced difficulties converging without the hurdle. For the hurdle negative binomial selection, we used a two-part process where the best model for the binomial presence/absence model was first determined for presence/absence data using the step model selection process. Then, we used a step model selection process to identify the best formulation for the count component with the determined hurdle model component.

Results

We deployed a total of 256 trap nets, 247 gillnets, 333 minnow traps, 66 hand seines, and 9 boat seine samples. We caught a total of 4,528 fish. The most abundant species was non-native white bass (1416 fish), followed by non-native black bullhead (1056) and common carp (1047). Trap nets caught at least one fish 95% of the time, gillnets 52%, boat seines 44%, minnow traps 32%, and hand seines 20%. The size distribution of fish caught was significantly different among the three most successful gears, (Kruskal-Wallis rank sum and pairwise Wilcoxon rank sum p-value <2.2E-16 for all pairings). However, the trap nets were able to capture most of the size variance we observed aside from the smallest individuals in the minnow traps (Figure 2a). Different net types also caught different compositions of species, with trap nets capturing black bullhead most frequently, gill nets capturing primarily white bass, and minnow traps primarily capturing fathead minnows (Figure 2b). Of the 1047 total carp caught, 856 were caught in one of the 228 trap nets that were suitable for further analysis, 46 were caught in trap nets that were not used for further analysis due to net failures where time elapsed could not be calculated, 92 were caught in gillnets, and 38 were caught in minnow traps (Figure 2b). All gear types caught less than one carp per unit of effort on average, except for the trap nets which caught 3.75 carp per unit of effort (one net night).

Similar to the commercial gears traditionally used in Utah Lake carp control, carp catch in the trap nets was dominated by large, age-seven plus individuals, however a few trap nets also caught a high number of small, age-zero individuals (Figure 3a). Interestingly, we were able to capture large numbers of other species in intermediate sizes for which we did not effectively catch carp (Figure 3b). Additionally, the age structure of catch varied across our different sampling sites (Figure 3c). We found that the catch data had more support by AIC with the hurdle negative binomial GLMM model than did the negative binomial GLMM for all ages of carp, small carp, and juvenile carp (Supplemental Table 1). Residual plots show a better model fit for all hurdle models (Supplemental Figure 1). As such, we focus our subsequent discussion on the results of the hurdle model.

Model components varied between the best fit models for different age groups (Figure 4; Table S2). Seasonal effects of year and month were included in both the hurdle and count components of all three models (Figure 4a; Table S2). A spatial effect of substrate was included in the hurdle component of all models while an effect of shoreline was included in the all ages and small carp models, but not the juvenile carp model (Figure 4b; Table S2). A lake level effect was included in the juvenile carp hurdle component but was only included in the small and all ages models as interactions (Figure 4c; Table S2). Trap positioning effects of whether a trap was set to shore and the depth of a trap were included in the juvenile carp hurdle component, while small and all ages hurdle components included a categorical distance from shore effect (Figure 4d; Table S2). Water depth was included in the all ages count component (Figure 4d; Table S2). Weather effects of wind speed and cloud cover were included in the juvenile hurdle component while only wind speed was included in the small and all ages hurdle components (Figure 4e; Table S2). Precipitation and cloud cover were included in the count component of all three models (Figure 4e; Table S2).

There were differences in the direction and intensity of temporal (Figure 4a) and spatial (Figure 4b) trends between models. Nets set in 2022 had a significant increase over 2021 and nets set in 2023 had a significant increase over 2022 in likelihood of encountering carp in the hurdle component of all models (Table S3), and in 2023 were 134 times, 270 times, and 125 times as likely to catch juvenile, small, and all ages of carp respective to 2021. Nets set in 2022 and 2023 were positively associated with carp counts in the small and all ages models, but were not significantly different from each other, and only 2022 had a significant positive effect in the juvenile model (Supplemental Table 2).

Juvenile carp were more likely to be caught in August than April (Figure 4a; Table S2). Small carp were more likely to be caught in June, August, or October, and nets were likely to catch larger numbers of small carp in August than April or October. In the all ages model, nets set in June and August had increased odds of catching any carp and were likely to catch greater numbers of carp than nets set in April, while nets in set in October were likely to catch fewer carp than those set in April. The effect of substrate was consistent across models, with nets set in rocky sites being less likely to encounter any carp than nets set in muddy sites for all models (Fig.4b; Table S2). However, rocky sites were only significantly different from sandy sites for adult carp (Supplemental Table 2). The only significant spatial effect was a lower likelihood of catching any carp on the western shoreline in the all ages hurdle component, but it was notably only significantly different from the eastern shoreline (Fig. 4b; Table S2).

Patterns in lake level (Figure 4c), trap positioning (Figure 4d), and weather (Figure 4e) effects also varied across models. An increase in lake level decreased the odds of catching juvenile carp, but for the small and all ages models this relationship was only significant for traps that were set against the shore or vegetation (Fig. 4c; Table S2). In the all ages hurdle model, an increase in water depth also increased the odds of catch as the lake level increased. Juvenile carp were 2.45 times as likely to be caught in a net that was set to shore as opposed to one that was not set to shore while small and all ages of carp were significantly less likely to be caught in traps that were between five and 100 meters of shore relative to nets set closer to shore, but were not significantly different from those set further than 100 m from shore (Supplemental Table 2). Juvenile carp were less likely to be caught when cloud cover increased, and small and all ages of carp were caught in lower numbers when cloud cover increased. Increasing precipitation had a minor negative effect on the count component of the all ages and juvenile carp models, but did not have a significant effect on the small carp model. Increasing wind speed had a slight positive effect on the probability of catching any small and juvenile age classes but did not have a significant effect in the all ages model.

Discussion

Successfully controlling a highly fecund invasive fish such as carp requires the use of multiple gears and an adaptive management strategy to target individuals across different life stages (Brown and Gilligan, 2014; Weber et al., 2016; Yick et al., 2021). Here, we evaluated alternative mechanical removal gears and identified spatio-temporal trends in the catch of cryptic juvenile and small adult carp to inform management efforts in Utah Lake. Trap nets were the most effective gear type for capturing carp, yet still had very low catch rates and would be difficult to effectively implement in control efforts. Juvenile and small adult carp catch was positively associated with years that had higher carp populations (Walsworth, Wallace, et al., 2023) and months that coincide with spawning timing. We were less likely to capture juvenile and small adult carp at sites with rocky substrate, and the western shoreline was the least likely place to catch carp in the all ages model, consistent with previous carp surveys in Utah Lake (Walsworth, Fadlovich, et al., 2023). Low numbers of juvenile and small adult carp combined with complex lake level relationships likely limit our ability to extrapolate from these findings, though we provide useful insights that can direct the focus of future research.

Catch quantity and composition varied between alternative mechanical removal gears in Utah Lake, but we did not identify a gear that was highly effective for catching large numbers of cryptic age classes of carp. While all of the gears we implemented have been applied effectively in other control programs (Rytwinski et al., 2018; Yick et al., 2021) our gear implementation was challenged by low lake levels, dense shoreline debris, or short set times (to minimize bycatch mortality) that have also reduced effectiveness in other studies (e.g., Diggle et al., 2012; Osborne, 2012). While the impact of different gear characteristics on catch composition is well documented in the literature (e.g. Fulton, 1893; Millar & Fryer, 1999; Rudstam et al., 1984), our results highlight the need to identify not only habitats that contain juvenile and small adult carp but gears that can effectively target them. Trap nets were our most effective gear, consistent with similar studies (Diggle et al., 2012), however, we observed relatively low trap net CPUE, which was likely impacted by our inability to set all nets against the shoreline due to low lake levels and shallow lake bathymetry. While trap nets were useful for collecting data on the spatial-temporal trends in Utah Lake, implementing trap nets in the carp control efforts would require immense effort in the form of many nets set out over many nights in order to compensate for low catch rates.

Temporal trends in juvenile and small carp catch are likely heavily influenced by an increase in carp population during 2022 and 2023 (Walsworth, Wallace, et al., 2023) and seasonal life history behaviors such as shoreline spawning, though both relationships interact with habitat effects. While we include daily average lake level as a covariate, seasonal variation in lake level may contribute to observed temporal trends. Increasing water levels result in increased shoreline habitat that can result in higher juvenile carp recruitment, are known to reduce harvest efficacy, but also improved our ability to properly deploy gears (Hicks & Ling, 2015; Pearson et al., 2022; Sorensen & Bajer, 2011). Seasonal patterns of all carp and small carp catch can likely be attributed to spawn timing, as we see the greatest increases in likelihood of catch corresponding with peak spawn timing (Bivens et al., 2021). Additionally, the seasonal differences in juvenile carp catch reflect the seasonality of young-of-year carp emergence and recruitment to the gears. These trends are consistent with seasonal variation of catch in other control programs (Weber et al., 2016; Yick et al., 2021) and our work supports the need to account for the timing of life history events when targeting multiple age classes. Additionally, our work suggests that trends differ between the presence/absence of carp and the count of carp in a trap and the impact of this difference should be considered when shaping future research and management targets (Miranda et al., 2023).

Our findings that carp were negatively associated with rocky sites differs from other carp control programs which found rocky sites to be a preferred secondary habitat for juvenile carp during low water years (Taylor et al., 2012). However, the negative association we saw with rocky and western sites in some models are consistent with other Utah Lake carp surveys (Watson et al., 2013; Walsworth, Fadlovich, et al., 2023) and represent the areas that have historically been avoided by commercial fishers. Our spatial findings are constrained by the limited number of rocky and sandy sites in our sample along with confounding lake level and trap positioning interactions as western and rocky sites tended to be deeper than other sites. Concentrated efforts on the western shore and at rocky sites may be able to better tease out the distribution in these habitats. However, increasing effort to gain clarity into negative associations may not be the best use of management resources when the goal is to find habitats that are associated with small and juvenile carp.

Low catch rates of our target size classes limited model performance and again highlight the difficulties faced by managers in large ecosystems especially when targeting cryptic individuals (Rejmánek & Pitcairn, 2002; Yick et al., 2021). We examined the effects of lake level, trap positioning, and weather in our model to account for factors influencing spatio-temporal carp distribution that were out of our control but acknowledge that the complex ways these factors interact with the behaviors of different life-stages makes it difficult to assess trends, especially across a short study period with highly variable lake levels. Capturing all of this variability would require expanding the number of sites and likely the frequency and length of our sampling efforts. We recognize that including slightly different trap positioning effects for the juvenile model complicates interpretation, however these simplified categories were necessary to obtain a model fit. Additionally, we are aware that both a hurdle and negative binomial model structure increase the risk of overfitting (Zuur et al., 2009) and were deliberate in our model development to ensure these structures were supported but still urge caution when extrapolating our results beyond our samples.

Though the range of potential control gears tested here was not exhaustive, the limited effectiveness of gears that have had success elsewhere (Diggle et al., 2012; Lechelt et al., 2017; Yick et al., 2021) suggests other avenues of controlling cryptic age classes may be worth exploring. One potential area of research is conditioning control efforts so harvest only occurs when the lake falls below a certain threshold (Pearson et al., 2022). Lake level conditioned control is being considered in Utah Lake and while high water years are associated with increased juvenile recruitment, our findings that juvenile carp are caught more often at low lake levels is an encouraging line of support for this method (Walsworth, Wallace, et al., 2023; Wallace et al., 2024). Non-mechanical removal methods should also be considered. Incorporating targeted poison bait, genetic technologies, and carp-specific viruses may offer a complementary management strategy to mechanical control, though each comes with its own set of limitations (Kennedy et al., 2018; McCormick at al., 2021; Schill et al., 2017).

Invasive species cause considerable economic and environmental impact (Early et al., 2016; Reid et al., 2005; Myers et al., 2000; Simberloff et al., 2013) and controlling carp, especially younger or smaller individuals, requires an intense effort that is often greater than what is financially or otherwise feasible within a management program (Weber et al., 2016; Britton et al., 2011). Evidence increasingly suggests that targeting carp and other prolific invasive species will require a large, coordinated effort (Yick et al., 2021; Walsworth, Wallace, et al., 2023). Short-term studies in highly dynamic environments such as Utah Lake may not be able to effectively characterize the spatio-temporal drivers of catch, as dynamic environmental conditions impact gear efficiency. One interesting future avenue that could inform subsequent spatio-temporal analysis of hard to capture size classes would be to conduct a power analysis to identify what level of sampling effort within and across years would be needed to effectively detect trends in juvenile carp abundance. However, targeting juvenile carp may not be the only strategy for effective control. If we assess which age classes of carp are most beneficial to target with control efforts, we can help establish which research and control efforts will be most beneficial (Fadlovich et al., *Chapter III*). The struggle of where to direct limited resources has long been recognized and echoed in the literature on invasive species' management (Baker et al., 2017; Simberloff, 2001; Simberloff, 2003), and studies like ours that shed light on when and where to direct effort are a critical piece in effective, science driven management.

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Tables and Figures

Table II-1. Description of categorical and continuous fixed effects terms that were included in model evaluation process. When applicable, reference subcategory is denoted by * and continuous effects are labelled. Effects in italics were not included in a best fit model. Parenthetical abbreviations are used in subsequent tables as needed.

Grouping	Categorical Effect	Description	Subcategories (reference subcategory *)
Temporal	Month (M)	Month of sampling	April*, June (6), August (8), October (10)
Temporal	Year (Y)	Year that sampling occurred	2021*, 2022, 2023
Temporal	*Sample Event*	A unique event number for each month, year sample event combination	August 2021 (1) through June 2023 (8)
Spatial	Shoreline (Shore)	Cardinal shore of lake	East*, North (N), South (S), West (W)
Spatial	Substrate (Subs)	Dominant substrate at site	Mud*, Rock (R), Sand (S)
Lake Level (LL)	Continuous	Continuous, scaled lake level response and interaction terms	Independent LL term and interaction between LL and continuous water depth (WD), between LL and categorical net positioning (Yes or No) against shoreline and vegetation.
Trap Positioning	Shore Distance (Dist)	How far trap was set from shoreline	Near <10m*, middle <100m (mid), far >100m (far)
Trap Positioning	Set to Shore (tS)	Was the trap set to shoreline?	No*, Yes
Trap Positioning	Set to Veg or Shore (tVS)	Was the trap set to a solid feature?	No*, Yes to shoreline or vegetation More flexible than tS to include nets set to dense vegetation that may function like shoreline.
Trap Positioning	Continuous	Continuous, scaled trap position and interaction terms	Scaled water depth (WD) at trap net mouth, scaled trap depth (TD) at trap net mouth,
Weather	Continuous	Continuous, scaled weather response terms	Air temperature (temperature, T), *water temperature*, average daily wind speed (wind speed, W), *average daily wind direction*, cloud cover (CC), *UV index*

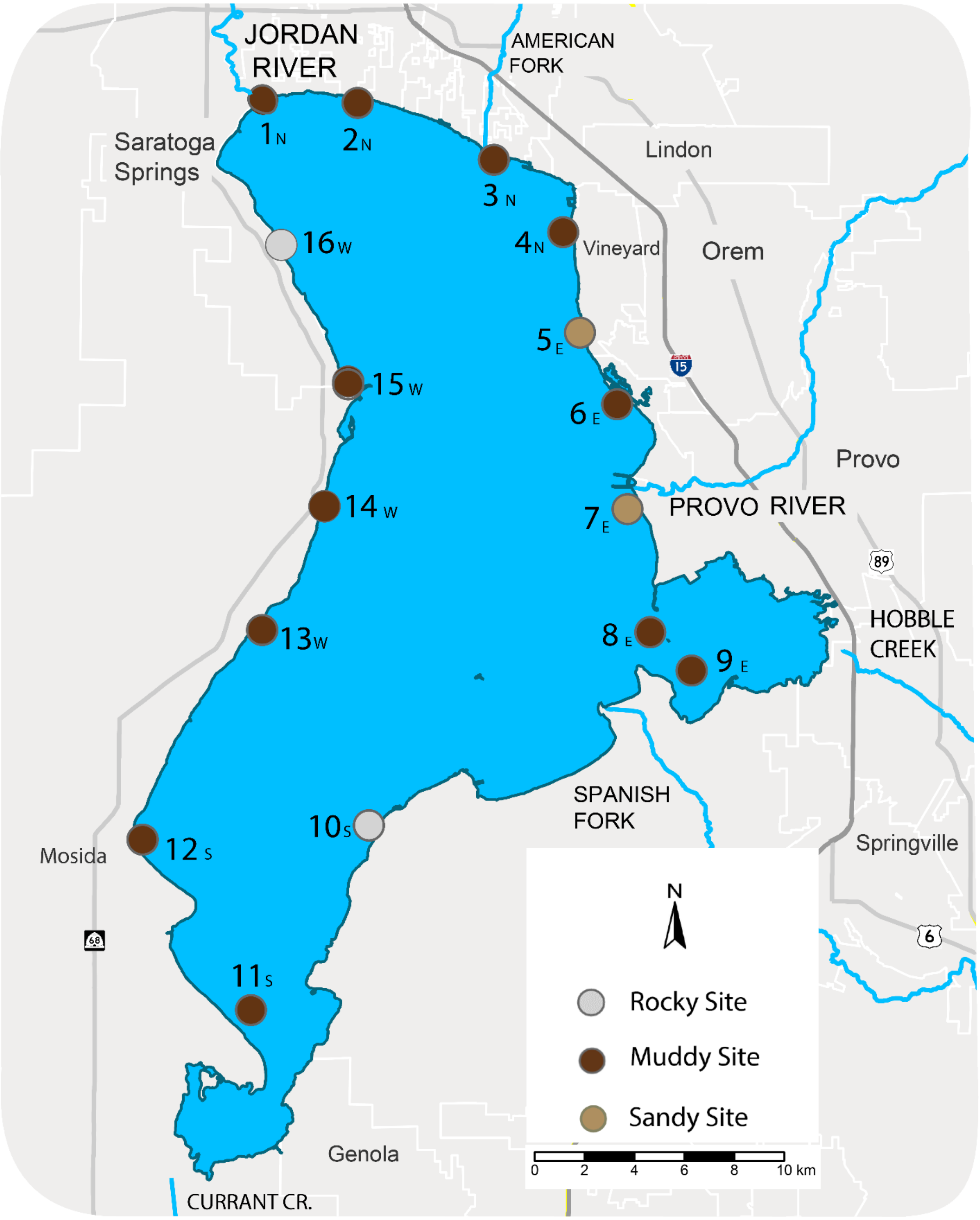


Figure II-1. Map of Utah Lake with points at standardized survey sites. Color denotes substrate type, letter denotes shore, and number is unique to site.

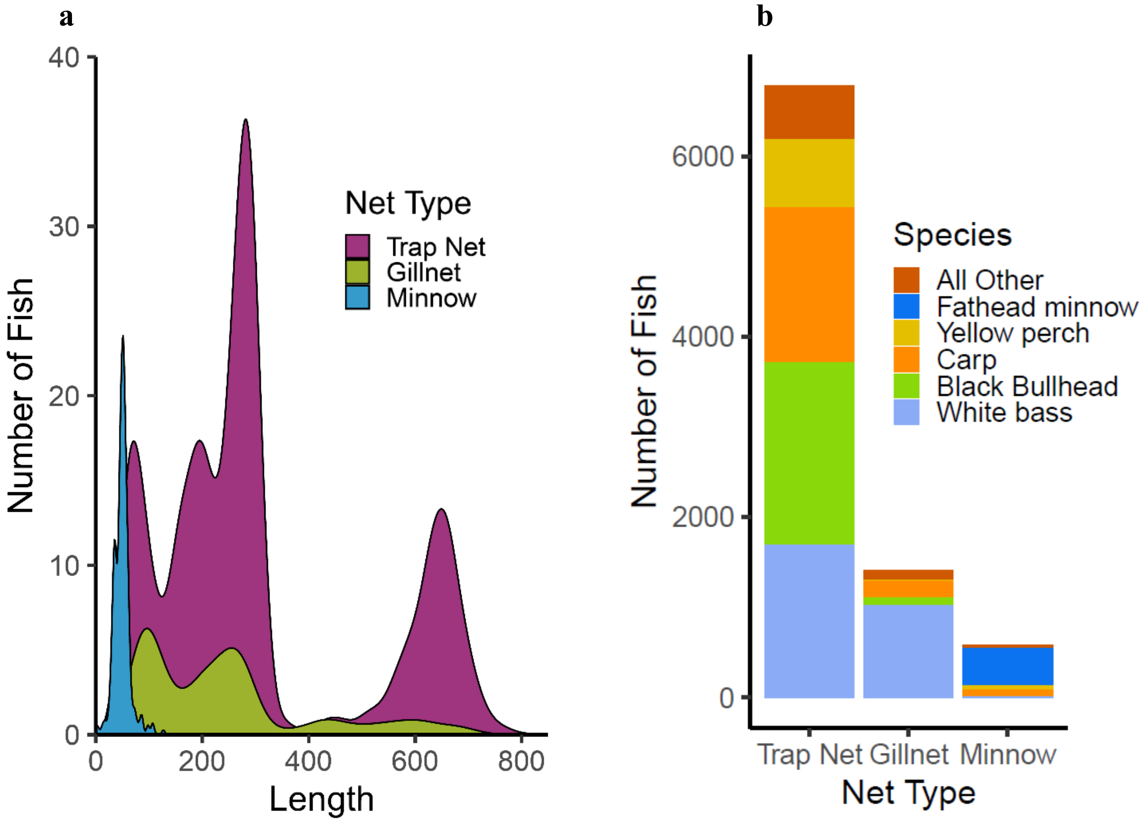


Figure II-2. Length frequency of fish by net type (a) and species composition by net type (b). Fish from the three most populated net types are included.

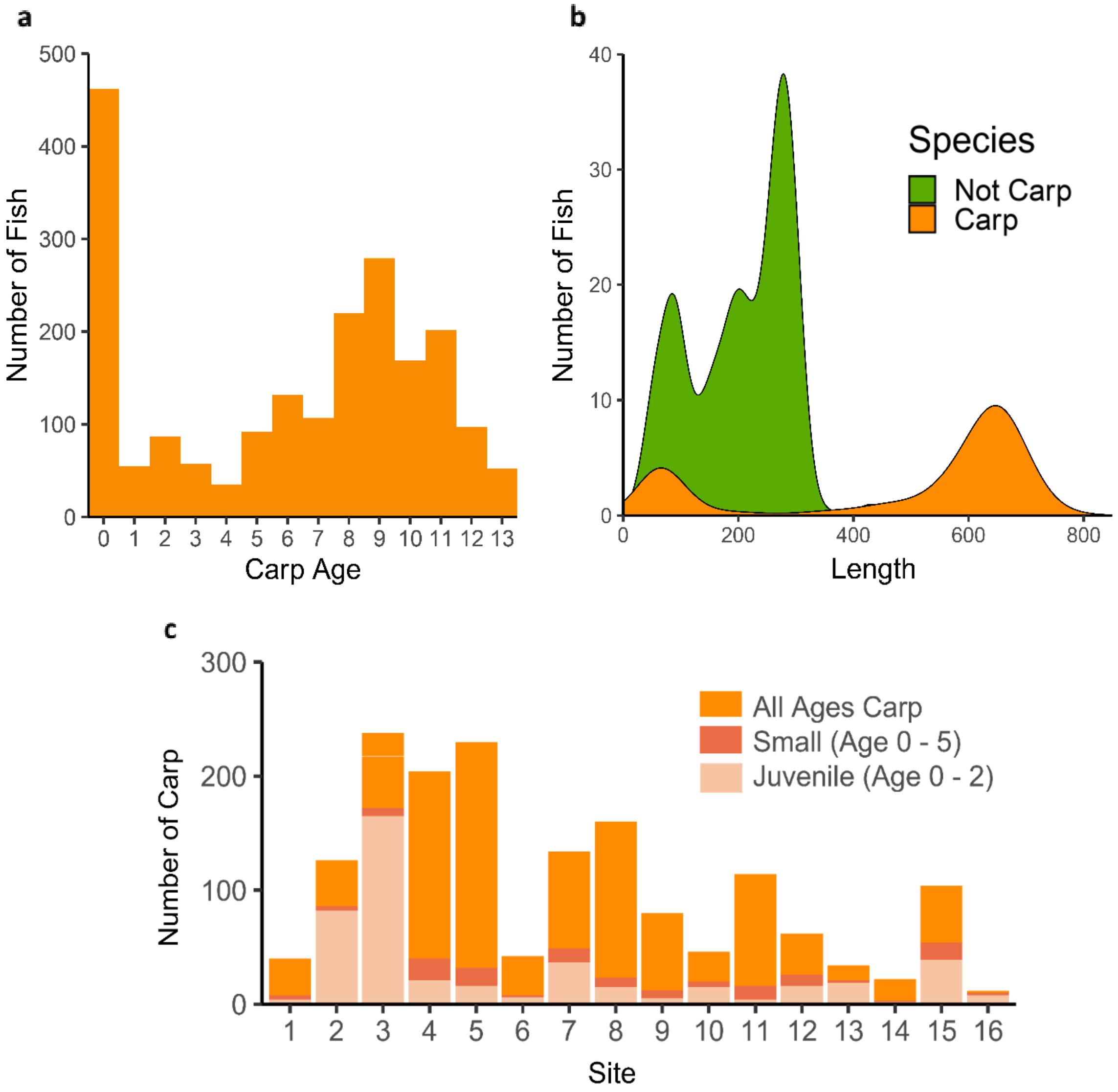


Figure II-3. Trap net carp catch by age (a), length frequency of carp versus all other species (b), and carp catch by age group at each survey site (c). Sites 1-4 are on the north shore, 5-9 on the east, 10-12 on the south, and 13-16 on the west. Site 16 and 10 are rocky, 5 and 7 are sandy, and all others are muddy.

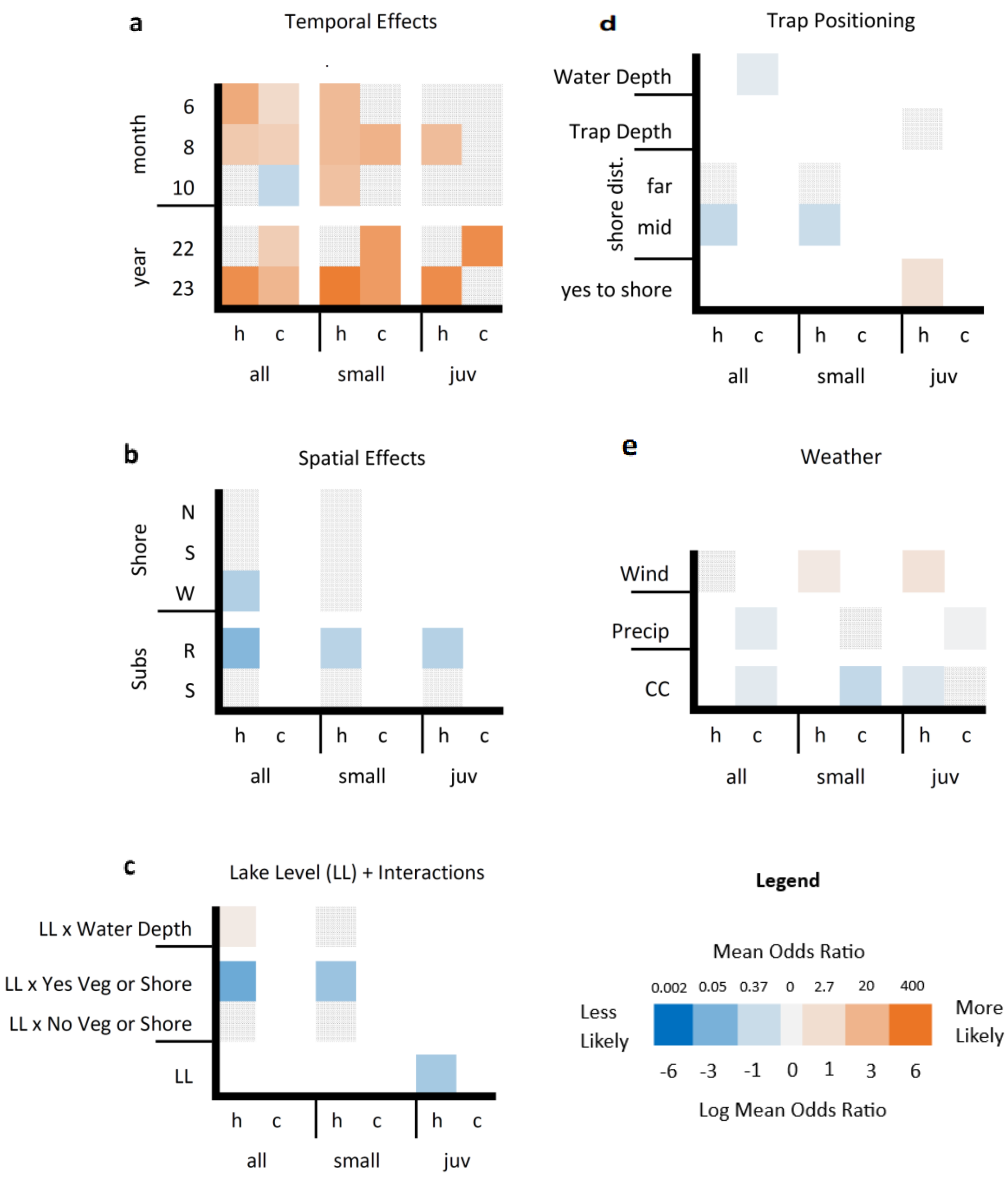
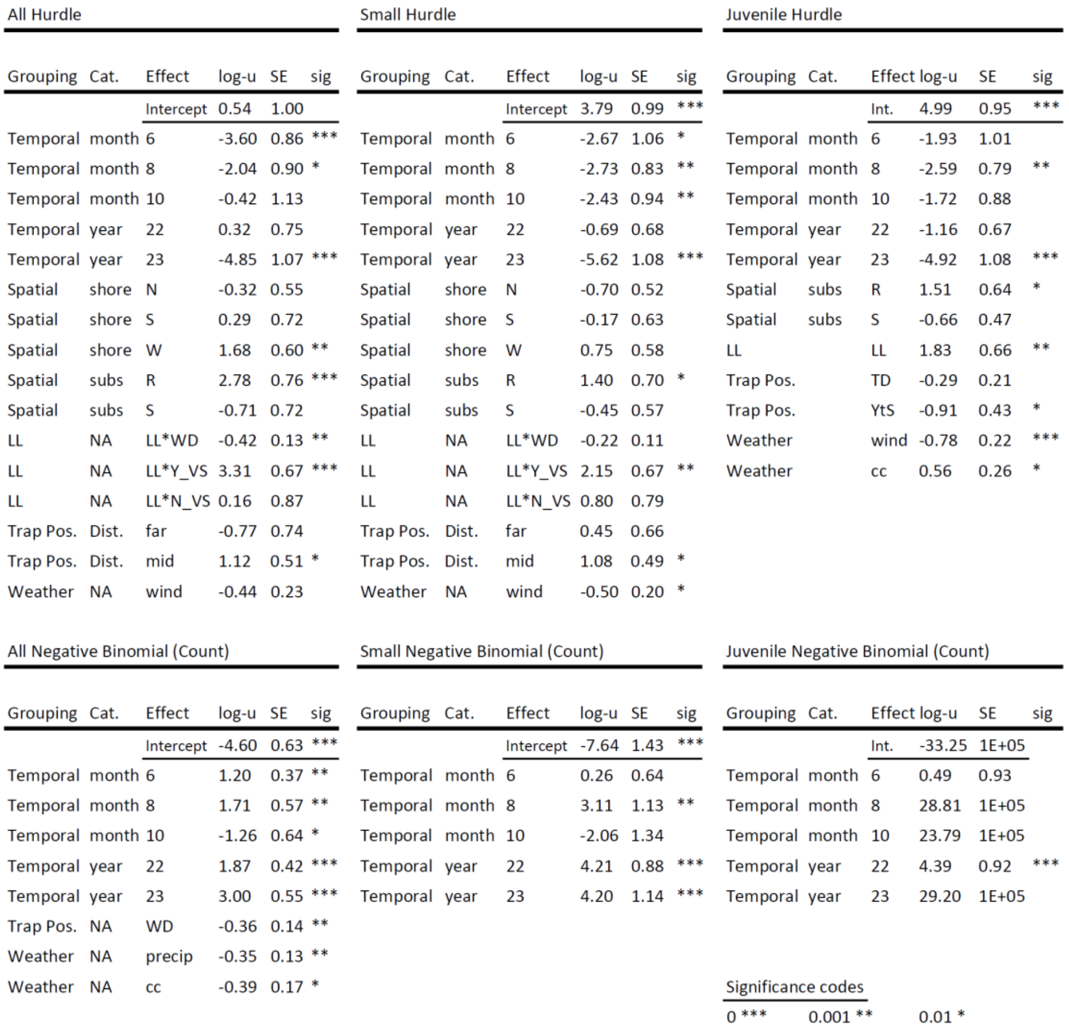


Figure II-4. Heat maps presenting grouped mixed effects model results for temporal (a), spatial (b), lake level (c), trap positioning (d), and weather (e) effects. For all plots, grey stipple denotes no significant effect, red is associated with a higher likelihood and blue with a lower likelihood, while the color intensity represents the strength of interaction. We denote categorical variables with vertical category labels. The x-axis for all plots provides the hurdle (h) and catch (c) components of the all ages (all), small, and juvenile (juv) carp models. Abbreviations on the y-axes are consistent with Table 1. We present the hurdle component as the likelihood of catch (1 minus likelihood of zero catch).

Supplemental Table 1: AIC comparison of the best fit hurdle negative binomial and standard negative binomial models for all age classes of carp.

Model	**NB Hurdle AIC**	**df**	**NB AIC**	**df**
All Ages	907.7	28	939.7	16
Small	533.3	27	544.3	13
Juvenile	413.0	23	425.3	16

Supplemental Table 2. Log mean effects, standard error, and significance for all covariates. The hurdle mean (log-u) is provided as in the output of glmmTMB, where it considers the likelihood of zero instead of the likelihood of catch. In Figure 3. we presented these values as the likelihood of catch (1 minus likelihood of zero) for clearer interpretation.



All Hurdle

Grouping	Cat.	Effect	log-u	SE	sig
		Intercept	0.54	1.00	
Temporal	month	6	-3.60	0.86	***
Temporal	month	8	-2.04	0.90	*
Temporal	month	10	-0.42	1.13	
Temporal	year	22	0.32	0.75	
Temporal	year	23	-4.85	1.07	***
Spatial	shore	N	-0.32	0.55	
Spatial	shore	S	0.29	0.72	
Spatial	shore	W	1.68	0.60	**
Spatial	subs	R	2.78	0.76	***
Spatial	subs	S	-0.71	0.72	
LL	NA	LL*WD	-0.42	0.13	**
LL	NA	LL*Y_VS	3.31	0.67	***
LL	NA	LL*N_VS	0.16	0.87	
Trap Pos.	Dist.	far	-0.77	0.74	
Trap Pos.	Dist.	mid	1.12	0.51	*
Weather	NA	wind	-0.44	0.23	

Small Hurdle

Grouping	Cat.	Effect	log-u	SE	sig
		Intercept	3.79	0.99	***
Temporal	month	6	-2.67	1.06	*
Temporal	month	8	-2.73	0.83	**
Temporal	month	10	-2.43	0.94	**
Temporal	year	22	-0.69	0.68	
Temporal	year	23	-5.62	1.08	***
Spatial	shore	N	-0.70	0.52	
Spatial	shore	S	-0.17	0.63	
Spatial	shore	W	0.75	0.58	
Spatial	subs	R	1.40	0.70	*
Spatial	subs	S	-0.45	0.57	
LL	NA	LL*WD	-0.22	0.11	
LL	NA	LL*Y_VS	2.15	0.67	**
LL	NA	LL*N_VS	0.80	0.79	
Trap Pos.	Dist.	far	0.45	0.66	
Trap Pos.	Dist.	mid	1.08	0.49	*
Weather	NA	wind	-0.50	0.20	*

Juvenile Hurdle

Grouping	Cat.	Effect	log-u	SE	sig
		Int.	4.99	0.95	***
Temporal	month	6	-1.93	1.01	
Temporal	month	8	-2.59	0.79	**
Temporal	month	10	-1.72	0.88	
Temporal	year	22	-1.16	0.67	
Temporal	year	23	-4.92	1.08	***
Spatial	subs	R	1.51	0.64	*
Spatial	subs	S	-0.66	0.47	
LL		LL	1.83	0.66	**
Trap Pos.		TD	-0.29	0.21	
Trap Pos.		YtS	-0.91	0.43	*
Weather		wind	-0.78	0.22	***
Weather		cc	0.56	0.26	*

All Negative Binomial (Count)

Grouping	Cat.	Effect	log-u	SE	sig
		Intercept	-4.60	0.63	***
Temporal	month	6	1.20	0.37	**
Temporal	month	8	1.71	0.57	**
Temporal	month	10	-1.26	0.64	*
Temporal	year	22	1.87	0.42	***
Temporal	year	23	3.00	0.55	***
Trap Pos.	NA	WD	-0.36	0.14	**
Weather	NA	precip	-0.35	0.13	**
Weather	NA	cc	-0.39	0.17	*

Small Negative Binomial (Count)

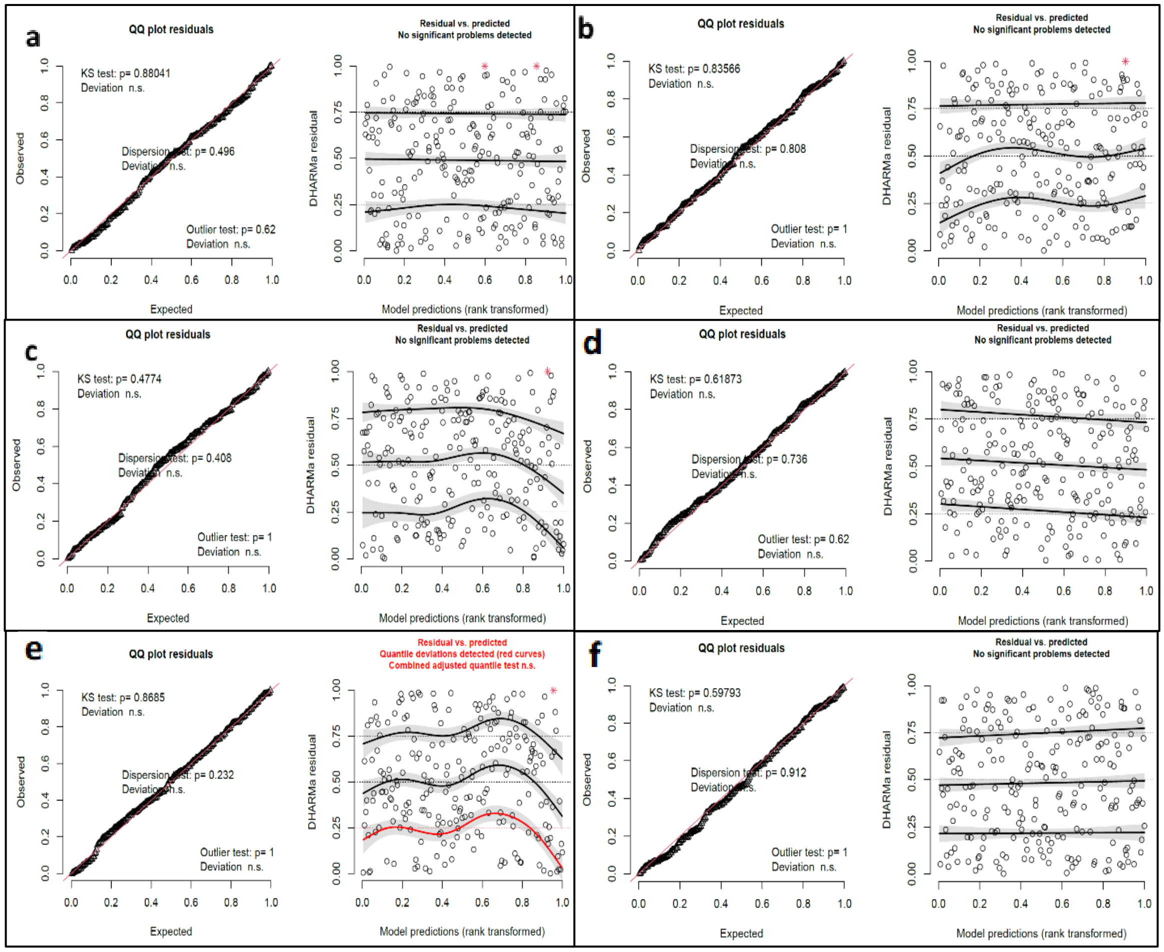
Grouping	Cat.	Effect	log-u	SE	sig
		Intercept	-7.64	1.43	***
Temporal	month	6	0.26	0.64	
Temporal	month	8	3.11	1.13	**
Temporal	month	10	-2.06	1.34	
Temporal	year	22	4.21	0.88	***
Temporal	year	23	4.20	1.14	***

Juvenile Negative Binomial (Count)

Grouping	Cat.	Effect	log-u	SE	sig
		Int.	-33.25	1E+05	
Temporal	month	6	0.49	0.93	
Temporal	month	8	28.81	1E+05	
Temporal	month	10	23.79	1E+05	
Temporal	year	22	4.39	0.92	***
Temporal	year	23	29.20	1E+05	

Significance codes

0 *** 0.001 ** 0.01 *



Supplemental Figure 1. Residual plots for the standard and hurdle best fit negative binomial models. Panel a is the all ages standard model, panel b is the all ages hurdle model, panel c is the small standard model, panel d is the small hurdle model, panel e is the juvenile standard model, and panel f is the juvenile hurdle model.

CHAPTER III

SIZE SELECTIVITY OF INVASIVE SPECIES REMOVAL GEARS INFLUENCES CONTROL EFFICACY

1 ABSTRACT

1) Invasive species control programs are often challenged by highly fecund invaders and size-selective removal gears, which can allow populations to recover due to compensatory recruitment. While commercial fisheries stock assessments have long explored how size/age- selectivity and fishing effort impact fish populations, these dynamics are not as frequently included in assessments of invasive fish control programs.
2) We use a simulation framework that integrates age-based gear selectivity and the widely implemented fisheries metric of maximum sustainable yield (MSY) to evaluate the effect of improving gear selectivity among cryptic age classes for invasive species population control. We apply this approach on common carp in Utah Lake, the location of one of the world's largest freshwater vertebrate species control programs.
3) Model simulations suggest that improving selectivity among cryptic, younger age classes has the potential to significantly reduce the amount of effort required to reach control targets. We found improving selectivity on younger, but mature, age classes allowed the carp population to remain below the control program's 75% biomass reduction target with only 2.5 times maximum historic effort, while further improving juvenile selectivity conferred minimal benefit.

4) Furthermore, we evaluated historic levels of control effort against both previously set management targets and theoretical sustainable fishing targets (MSY). The historic level of fishing effort was below MSY regardless of selectivity, suggesting the control program would be harvesting at a sustainable rate even if gear selectivity were improved for cryptic age classes.
5) *Synthesis and applications.* Controlling highly fecund invasive species becomes much more feasible if an approach that targets all adult age classes can be identified. Incorporating sustainable harvest metrics into simulation models of invasive species populations provides a framework for evaluating a harvest control program's ability to overcome density-dependent processes and achieve management objectives.

2 INTRODUCTION

Invasive species are one of the greatest threats to global biodiversity (Early et al., 2016; Reid et al., 2005; Vitousek et al., 1997) and finding ways to mitigate their impacts is of interest to managers globally (Britton et al., 2011; Doherty et al., 2016; Simberloff, 2001). In large, interconnected systems, eradication is unlikely (Green & Grosholz, 2021; Rejmánek & Pitcairn, 2002; Simberloff, 2003) and managers often aim to suppress the invasive population to a level that mitigates negative ecosystem impacts (Manchester & Bullock, 2000; Weber et al., 2016). In invasive fish management, physical removal or harvest is the most common strategy for population suppression (Rytwinski et al., 2018). Suppression efforts are often challenged by compensatory processes, as the intensity of control efforts are not high enough to successfully overcome density-dependent recruitment and survival (Weber et al., 2016, Zipkin et al., 2008). Incorporating these density-dependent processes into management models can allow for better predictions of control outcomes (Shyu et al., 2013; Walsworth et al., 2020; Weber et al., 2011).

Taking lessons from fisheries management, where much work has been done concerning the density dependence (Jensen et al., 2012, Rose et al., 2001; Svedäng & Hornborg, 2014) and sustainable exploitation of populations (Frank & Brickman, 2001; Hilborn & Walters, 1992; Schaefer, 1954), may shed light on approaches to improve invasive control success. Density-dependent growth, survival, and reproduction produce a surplus biomass at intermediate population densities, forming the basis for sustainable commercial fisheries harvest (Beverton & Holt, 1957; Schaefer, 1954; Svedäng & Hornborg, 2014) but potentially hindering the efforts of invasive species control (Yick et al., 2021; Zipkin et al., 2009). Fisheries managers have long relied on the concept of maximum sustainable yield (MSY) and F_{msy}, the fishing mortality that maximizes biomass that can be sustainably harvested indefinitely (Frank & Brickman, 2001; Hilborn & Walters, 1992; Schaefer, 1954), which serves as a useful reference point when comparing alternative management objectives (Hilborn & Walters, 1992; Hilborn et al., 2022; Vasilakopoulos et al., 2020) and remains the basis of fisheries management policy in many countries (ICES, 2011; Worm et al., 2009).

Fisheries management has traditionally relied on the manipulation of exploitation rates to achieve MSY, although the concurrent impact of population selectivity, the proportion of fish at a given size (or age) that are vulnerable to fishing (Millar & Fryer, 1999), has long been recognized (Beverton & Holt, 1957; Hilborn & Walters, 1992; ICES, 2011) and has been increasingly included in contemporary fisheries advice (Ben-Hasan et al., 2021; Scott & Sampson, 2011; Vasilakopoulos et al., 2020). Population selectivity (hereafter "selectivity") encompasses both contact selectivity, influenced by gear selection and mesh size, and available selectivity, influenced by the timing and location of fishing activities (Millar & Fryer, 1999; Quinn & Deriso, 1999; Sampson & Scott, 2012), and is represented in terms of length, age, or life stage depending on the management context (Millar & Fryer, 1999; Scott & Sampson, 2011). Selecting for older/larger fish supports sustainable harvest initiatives if fish are not susceptible to harvest until after they mature and have the opportunity to reproduce, thus avoiding recruitment overfishing (Scott & Sampson, 2011; Vasilakopoulos et al., 2016). However, selecting for older/larger fish can be problematic in invasive species management if it promotes high population levels despite high harvest effort (Britton et al., 2011; Walsworth et al., 2020; Yick et al., 2021).

Invasive species with high population densities, low survival rates, and high fecundity are often able to compensate for adult selective harvest (Sedinger et al., 2007; Weber et al., 2016; Zipkin et al., 2009). The common carp (*Cyprinus carpio*; *hereafter* "carp"), considered to be one of the most prevalent and damaging invasive species in the world (Sorensen & Bajer, 2011; Hicks & Ling, 2015; Lowe et al., 2000), is a highly fecund fish frequently exhibiting compensatory recruitment in response to harvest (Walsworth et al., 2020; Weber & Brown, 2012; Weber et al., 2016). While carp are among the freshwater fishes most commonly subject to documented mechanical removal efforts (Rytwinski et al., 2018), successful control or eradication is rare and limited to relatively small lake systems (Dauphinais et al., 2018; Yick et al., 2021). It has been suggested that targeting all age classes is essential to effective control (Weber et al., 2011;

Yick et al., 2021), yet targeting the youngest age classes of fish is often inefficient and expensive.

Here, we examine the relative effect of increasing selectivity on these cryptic, younger age classes to evaluate the tradeoffs between improving selectivity and increasing fishing effort. We use a simulation model fit to empirical data to assess (1) how control efficacy improves with increased selectivity of younger age classes and (2) identify the age-classes that provide the greatest control benefit when targeted. This approach can help managers evaluate the relative benefits of investing in improving gear selectivity and increasing fishing effort. This model serves as a management tool for evaluating the control potential of alternative removal gears and strategies in systems where mechanical invasive species control efforts are challenged by highly selective harvests and compensatory recruitment.

3 MATERIALS AND METHODS

3.1 Site description

Utah Lake (Fig. 1) is a large (~380 km^2), shallow (average depth 3.2 m) lake located in Utah County, Utah, USA. In the early 2000s, non-native carp accounted for over 90% of the lake's fish biomass (SWCA, 2002) and have contributed to reduced water quality, altered food web dynamics (King et al., 2024), and pose a threat to the endemic and federally threatened June sucker (*Chasmistes liorus*). Since complete carp eradication was deemed infeasible due to the lake's size and connectivity, managers began carp removal efforts in 2009 with a target to reduce carp biomass by 75% (SWCA, 2002; 2005; Walsworth et al., 2020) which reports suggested could be achieved in five years, would suppress the population's reproductive potential, and would allow for a reduction in harvest once the target was achieved (SWCA, 2005; 2006).

While the control efforts are estimated to have removed more than 13,000 tons of carp and drove an initial population decline, large recruitment events that are partially driven by recent high lake level conditions have contributed to subsequent population recovery (Walsworth et al., 2020; Walsworth, Wallace, et al., 2023). The commercial fishing seines being used in Utah Lake carp control efforts are the most commonly implemented carp control gear (Yick et al., 2021) but have minimal impact on cryptic age zero to five carp, while the carp are reproductively mature by age three (Walsworth et al., 2020; Walsworth, Fadlovich, et al., 2023). Previous modeling work suggests that effectively targeting juvenile carp could improve the likelihood of successful control but did not evaluate more subtle changes to selectivity such as targeting small adults (Walsworth et al., 2020).

3.2 Data

3.2.1 Standardized commercial seine sampling

Since 2012, standardized annual surveys using the same commercial gear applied during removal efforts, a 184 m long, 3 m deep commercial beach seine with 1½-inch square mesh (*hereafter* "large mesh" seines) have been conducted by Utah State University, the Utah Division of Wildlife Resources, and Loy Fisheries. Beginning in 2020, a subset of hauls were conducted using a "small mesh" seine with ¾-inch mesh. While commercial hauls were conducted in targeted locations, between 27 and 43 (depending on site accessibility) standardized seine samples were collected from a consistent set of spatially stratified sites around the lake perimeter each year (see Landom et al., 2014).

For each seine sample, the total number of carp captured was documented and a subsample (up to 30 individuals) was randomly selected for body length and weight measurements. The age-composition of carp caught was calculated with a probabilistic approach based on fitting a Von Bertalanffy growth curve to length-at-age data (ages estimated from the dorsal spines of a subset of carp) and length-frequency data (see Walsworth et al., 2020; Walsworth, Wallace, et al., 2023 for a full description of methods). Data pertaining to historic carp commercial fisheries effort was provided by the June Sucker Recovery Implementation Program.

3.2.2 Carp population estimates

We take our estimates of carp abundance-at-age from a statistical catch-at-age model developed using standardized seine sampling catches, commercial fisheries effort, commercial removal data, and lake level measurements (see Walsworth et al., 2020 for a full model description, Walsworth & Landom, 2021 for an updated catchability component, and Walsworth, Wallace, et al., 2023 for updated abundance estimates). The model follows a standard age-structured framework (Caswell, 2001) with the addition of a Ricker stock-recruitment model and incorporates parameters for fishing effort, age-based gear selectivity, and lake level effects on both catchability and recruitment. Our simulation model modifies the published carp population model with alternative selectivity scenarios, described below.

3.3 Gear selectivity analysis

To evaluate existing gear selectivity, we first calculate observed selectivity-at-age for all age-by-haul combinations of the 2021 and 2022 small and large mesh seine hauls:

$$\hat{s}_{a,g,h} = \frac{ln\left(1 - \frac{C_{a,g,h}}{N_a}\right)}{-q}$$

where $\hat{s}_{a,g,h}$ is a scalar of estimated selectivity at age a for haul h of gear g, $C_{a,g,h}$ is the catch of age a carp in haul h of gear g, N_a is the estimated abundance at age a, and q is the estimated catchability coefficient. $C_{a,g,h}$ was obtained from the standardized commercial seine surveys and N_a and q estimates were taken from outputs of the most recent Utah Lake carp statistical catch-at-age model (Walsworth, Wallace, et al., 2023). We then fit an age-selectivity model to these haul-specific selectivities-at-age, which assumed a sigmoidal relationship, as found in Walsworth et al. (2020):

$$s_{a,g} = \frac{1}{1 + e^{\left(\frac{-ln(19)\left(a - A_g^{50}\right)}{A_g^{95} - A_g^{50}}\right)}}$$

where $s_{a,g}$ is the mean selectivity of gear g for individuals of age a, A^{50} is the age at which gear g has 50% selectivity, and A^{95} is the age at which gear g has 95% selectivity. We used a Bayesian hierarchical framework to determine the best parameter values, assuming beta-distributed errors:

$$\hat{s}_{a,g,h} \sim Beta\left(\alpha_{a,g}, \beta_{a,g}\right)$$

$$\alpha_{a,g} = \left(\frac{s_{a,g}\left(1 - s_{a,g}\right)}{\sigma_{a,g}^2} - 1\right) s_{a,g}$$

$$\beta_{a,g} = \left(\frac{s_{a,g}\left(1 - s_{a,g}\right)}{\sigma_{a,g}^2} - 1\right)\left(1 - s_{a,g}\right)$$

where $\alpha_{a,g}$ and $\beta_{a,g}$ are shape parameters for the beta distribution of selectivity at age *a* and gear *g*, and $\sigma_{a,g}^2$ is the estimated variance in selectivity at age *a* for gear *g*. We fit the selectivity model in JAGS (Just Another Gibbs Sampler; Plummer, 2003), implemented with the R2jags package (Su & Yajima, 2021) through the R Statistical Computing Environment (R Core Team, 2022).

3.4 Alternative selectivity simulations

3.4.1 Alternative selectivity scenarios

We investigated hypothetical selectivity scenarios to help determine which cryptic age classes are important to target with control efforts. The large mesh gear selectivity estimated above served as our baseline selectivity for the alternative selectivity simulations. We generated alternative gear selectivity scenarios in which sequentially younger age classes are increasingly vulnerable to removal gears, by reducing the baseline A^{50} and A^{95} values by one age at a time and calculating mean selectivity at age using the sigmoidal relationship described above for a total of ten additional selectivity scenarios. To ensure that relative catchability remained constant across all scenarios, we scaled each selectivity scenario to the baseline maximum selectivity at age:

$$A_z^{50} = A_0^{50} - z$$

$$A_z^{95} = A_0^{95} - z$$

$$s_{a,z} = \frac{1}{1 + e^{\left(\frac{-ln(19)\left(a - A_z^{50}\right)}{A_z^{95} - A_z^{50}}\right)}} * \frac{s_{max,z}}{s_{max,0}}$$

where A_z^{50} is the age with 50% selectivity for scenario z, A_z^{95} is the age with 95% selectivity for scenario z, $s_{a,z}$ is the mean selectivity at age a for scenario z, $s_{max,z}$ is the highest selectivity-at-age class for scenario z, and $s_{max,0}$ is the highest selectivity-at-age from the baseline selectivity curve (Fig. 2).

Gear selectivity model outputs of variance were used for the baseline selectivity scenario. To determine variances for all other scenarios, we fit a second order polynomial to baseline mean selectivity-at-age and variance data:

$$\sigma_{s_{a,z}} = \left(0.436 * s_{a,z}\right) - \left(0.408 * {s_{a,z}}^2\right)$$

where $\sigma_{s_{a,z}}$ is the variance for the selectivity $s_{a,z}$ at age a and simulation scenario z. This regression fit the baseline data well (adjusted R-squared 0.9837). If predicted $\sigma_{s_{a,z}}$ values exceed the constraints of the beta distribution:

$$\sigma_{s_{max}} = s_{a,z} * (1 - s_{a,z}),$$

the variance was corrected with:

$$\sigma_{s_{a,z}} = \sigma_{s_{max}} - 0.1 * \sigma_{s_{max}}$$

where $\sigma_{s_{max}}$ is the maximum selectivity allowed by the beta distribution for the mean selectivity at age, $s_{a,z}$.

For each selectivity scenario, the mean scenario selectivity was calculated to allow for graphical comparison:

$$\bar{s}_z = \frac{\sum_{a=1}^{8} s_{a,z}}{8}$$

where each selectivity scenario, z, has a mean scenario selectivity value, $\bar{s}_z$.

For each selectivity scenario, we simulated the carp population response to varying levels of control effort, E. Each selectivity scenario was simulated with 61 levels of effort where the number of seine hauls, h, ranged from historic mean to 100 times historic maximum effort (Table S1).

3.4.2 Simulating carp population response

We modified the selectivity component of the underlying statistical catch-at-age model to simulate the carp population response to each selectivity scenario and effort level, for a total of 671 combinations. For all ages in each combination, an age-based effort by selectivity term, $k_{E,a,z}$, was obtained by summing h draws from a beta distribution with mean $s_{a,z}$ and variance $\sigma_{s_{a,z}}$. Annual harvest at age for each selectivity and effort combination was calculated as:

$$H_{z,a,E,t} = N_{a,t} * (1 - e^{-q * k_{E,a,z}}) * w_a$$

where $N_{a,t}$ is the abundance of carp at age a in time t, w_a is the average weight of a carp age a, and q is a catchability coefficient obtained from the underlying statistical catch-at-age model (Walsworth et al., 2020; Walsworth, Wallace, et al., 2023). For each selectivity scenario including the baseline, we simulated 1000 model iterations, each projecting the population 50 years into the future. To obtain annual carp biomass estimates, we identified the median, 50%, and 90% confidence interval for $N_{a,t}$ across model iterations and multiplied by a mean Utah Lake carp weight-at-age (Walsworth et al., 2020; Walsworth, Wallace, et al., 2023). All simulations were run in the R Statistical Computing Environment (R Core Team, 2022).

3.4.3 Evaluating control potential

To evaluate the control potential of our selectivity scenarios, we first determined the average carp biomass and average harvest biomass between model year 25 and 50 for each combination of selectivity and effort. We evaluated years 25 to 50 to strike a balance between the urgency of invasive species management (Simberloff, 2003) and the stable population dynamics evaluated in traditional fisheries management (Hilborn & Walters, 1992).

To compare all selectivity scenarios, we determined $E_{target,z}$, the level of effort required for average carp biomass to meet the target biomass (25% of historic maximum biomass) in 50% of model iterations for scenario z. We then evaluated the increase in operational costs that would be associated with increasing fishing effort. The cost for our baseline maximum historic effort scenario was obtained by multiplying 131, the number of fishing days in the maximum effort year, by $4,000, the most recent cost per day of fishing, to obtain a baseline cost of $524,000. We then multiplied this baseline cost by the number of times maximum historic effort required to reach our objectives since increasing effort would require hiring additional crews with commensurate operation costs. We also determined $E_{msy,z}$, the level of effort that provides the maximum average harvest biomass, MSY, in 50% of model iterations for scenario z.

4 RESULTS

4.1 Gear selectivity analysis

Utah Lake carp seine gear selectivity is much greater for older age classes, and essentially zero for juvenile carp age-classes. The gear selectivity model fit to the large mesh seine annual survey hauls had a model median A^{95} of 8.78 years (95% confidence interval 8.77 to 8.98) and A^{50} of 5.5 years (95% confidence interval 5.41 to 5.61), meaning that a carp aged five and below is selected for less than half of the time (Fig. S1). Selectivity for the small mesh seine showed no significant difference from that of the large mesh seines (Fig. S1), having a model median A^{50} of 5.52 years (95% confidence interval from 5.29 to 5.69) and A^{95} of 8.8 years (95% confidence interval from 8.53 to 8.99). Because there is no meaningful difference in selectivity, we only evaluated the large mesh selectivity in subsequent simulations.

4.2 Alternative selectivity simulations

4.2.1 Simulating carp population response

The Utah Lake carp population is unlikely to be maintained below the management target with the current gear selectivity and effort. Simulation results show that with baseline large mesh selectivity and historic maximum effort, the median population estimate reduces from current day, but stabilises before reaching the target (Fig. 3). There is a modest chance of control success in any given year, with an average of 39% of model iterations meeting the control target after ten years.

4.2.2 Evaluating control potential

Effort would have to significantly increase from historic levels for the current gear to achieve and maintain target biomass. The large mesh seine baseline selectivity scenario achieves $E_{target,0}$, the median level of effort required to meet the target across simulation years 25-50 on average, at 17 times maximum historic effort (Fig. 4a). This would increase the operation cost from the historic baseline of \$524,000 to \$8,908,000. More than 80 times maximum historic effort is required for 95% of model iterations to reach target biomass, which could increase costs to \$41,920,000. Unsuprisingly, the level of effort to achieve the target biomass is greater than the effort required to harvest maximum sustainable yield. The baseline selectivity scenario reaches $E_{msy,0}$, the level of effort that achieves a maximum average carp harvest biomass, at 11 times maximum historic effort (Fig. 4b). To achieve MSY for 95% of model iterations, it would require 24 times maximum historic effort.

Improving gear selectivity for younger age classes reduced the level of effort needed for control efforts to achieve either biomass reduction goals or MSY, but improvements were minimal once all adult age classes were selected by the gear (Fig. 5). Small increases in selectivity drove substantial decreases in the level of effort required to achieve biomass targets ($E_{target,1}$ = 9, $E_{target,2}$= 5.5, $E_{msy,1}$ = 7, $E_{msy,2}$ = 4). After the fifth selectivity scenario, when selectivity was above 0.5 for all adult age classes and additional scenarios primarily improved selectivity in juvenile age classes (Fig. 1). Further improving selectivity resulted in minimal reductions to $E_{target,v}$ and $E_{msy,v}$ (Fig. 5). All scenarios with average selectivity above 0.5 would require between 1.5x or 2.5x increase in maximum historic effort, which would result in an estimated operational cost between \$786,000 and \$1,310,000. $E_{target,v}$ and $E_{msy,v}$ remained constant once adult selectivity reached a value of at least 0.75 for all adult ages (Figs 2,5).

No selectivity scenarios were able to achieve target biomass with historic mean effort, and all scenarios were fishing sustainably and below F_{msy} at historic mean effort. The lowest $E_{target,v}$, seen in all five selectivity scenarios where average selectivity was greater than 0.7, was 1.5 times maximum historic effort. While all scenarios reached $E_{msy,v}$ before $E_{target,v}$, the difference between the two decreased as selectivity improved.

Once all adult ages classes were close to optimally selected, in the fifth scenario, $E_{target,v}$ only required an additional 0.5 times maximum historic effort than to achieve $E_{msy,v}$.

5 DISCUSSION

Our simulations provide evidence that small improvements in selectivity can have big impacts on the level of effort required to reach invasive species control targets, but that diminishing returns eventually limit these benefits. Control becomes feasible once all reproductive-aged carp are optimally selected for, suggesting that effectively targeting all adult age classes is key to invasive species control efforts while targeting immature age classes provides little additional benefit. While selectivity had a significant impact on control efficacy, as is the case in commercial fisheries management it is the combination of selectivity and fishing effort that impact the standing population size and harvest potential (Vasilakopoulos et al., 2016). Our results show that the Utah Lake carp control program is fishing well below the level of effort needed to reach the control target and is indeed well below the level of effort needed to exceed MSY. Not only are increases in effort alone unlikely to achieve the control target but increases in effort that remain below MSY could further intensify the density-dependent population responses (Hilborn & Walters, 1992) if selectivity for younger adult carp does not improve.

Including metrics that evaluate density-dependent population responses allows for a more realistic assessment of the efficacy of harvest management for invasive species control. We show how selectivity and MSY, a traditional fisheries management target which evaluates the long-term viability of a population under harvest pressure (Hilborn & Walters, 1992), can be incorporated into an invasive species population modeling framework to better evaluate control potential. Previous work has shown that overcoming density-dependent processes is difficult when attempting to control highly fecund invasive species (Zipkin et al., 2009) such as carp, especially when highly age-selective gears are used (Walsworth et al., 2020; Weber et al., 2011). Findings from simulation models have urged the inclusion of selectivity metrics in commercial fisheries stock assessments (Scott & Sampson, 2011; Vasilakopoulos et al., 2020) and our simulations suggest that including selectivity and effort would confer similar benefit to managers evaluating the control potential of invasive species populations.

While it has been proposed that successful carp control requires targeting all age classes (Yick et al., 2021), we show that effectively targeting carp of reproductive age has the potential to be a viable control strategy. We saw large reductions in the effort required to reach a control target with small increases in the selectivity of younger fish that leveled off once all adult ages were effectively targeted. Similar patterns are seen in commercial fisheries, where small decreases in the selectivity of younger fish can increase sustainable harvest (Scott & Sampson, 2011), as avoiding younger fish can help avoid recruitment overfishing (Ben-Hasan et al., 2021; Myers et al., 1994; Vasilakopoulos et al., 2020). Our model suggests effort levels would need to be increased 17 times over to achieve control success in Utah Lake without improving selectivity. Such increases would be difficult to achieve given the current financial resources allocated to this management objective. Identifying gears that improve selectivity of cryptic younger adult age classes could significantly reduce the cost of effective control and should be a management priority.

While our simulation framework highlights the substantial benefits of increasing selectivity on mature age classes for effective control, we make some necessary assumptions in our model that should be considered when interpreting our results. We do not test for or incorporate temporal shifts in maturity or natural mortality in our model in response to fishing mortality, though these responses are well documented in commercial fisheries (Kuparinen & Merilä, 2007) and may be beneficial to consider in long-term management scenarios. Additionally, we have not identified a gear that demonstrates improved selectivity in Utah Lake as the small mesh seine tested during standardized annual surveys did not improve selectivity. The inability to target younger fish is a common attribute of commercial seines (Rytwinki et al., 2018; Sun et al., 2022; Weber et al., 2011), which suggests that modifying selectivity will require alternative control methods and a shift in the location or timing of control efforts.

Management resources are not infinite, and simulation frameworks such as the one presented herein can help managers anticipate the scale of effort that will be required to meet a management objective. Our simulation framework allows us to rapidly evaluate a large number of alternative control scenarios for their efficacy, and like other simulation frameworks, is a useful tool for evaluating the control potential of management actions and objectives (van Poorten et al., 2018; Vasilakopoulos et al., 2020; Weber et al., 2011). While population suppression is often seen as financially and ecologically more feasible than eradication (Manchester & Bullock, 2000), managers who increase control efforts to meet a biomass target run the risk of strengthening a population's density-dependent responses (Grosholz et al., 2021; Zipkin et al., 2008) and increasing costs without reaching the management objective (Scott & Sampson, 2011; Weber et al., 2016). Using modeling tools and metrics developed for fisheries management, where the density-dependent response of harvested populations has long been of interest (Beverton & Holt, 1957; Quinn & Deriso, 1999; Reed, 1980) can provide insights when evaluating the trade-offs between selectivity, effort, and population response for invasive species control programs. Ultimately, these models can help managers determine if the level of effort and length of time required for successful control are feasible given the available resources.

Invasive species management is a difficult task not limited to freshwater systems (Molnar et al., 2008) or fish populations (Lowe et al., 2000; Sakai et al., 2001; Simberloff, 2011) and can benefit from forecasting techniques used in other disciplines. It is widely acknowledged that selective gears make it difficult to overcome density-dependent populations of invasive species, yet few viable management strategies exist for evaluating population-level control measures that overcome these challenges (Yick et al., 2021; Zipkin et al., 2009). While density-dependent responses are well documented in fisheries management (Britton et al., 2011; Hilborn & Walters, 1992; Rose et al., 2001) the need to consider demographic structure and density-dependent responses has also been highlighted in the conservation of diverse taxa (Comita et al., 2014; Sedinger et al., 2007) and control of invasive populations (Shyu et al., 2013; Zipkin et al., 2009). Using simulation models to evaluate population responses and control potential of different management strategies can help managers identify which available management methods can work within social and economic constraints to overcome the demographic challenges presented by invasive species.

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7 TABLES AND FIGURES

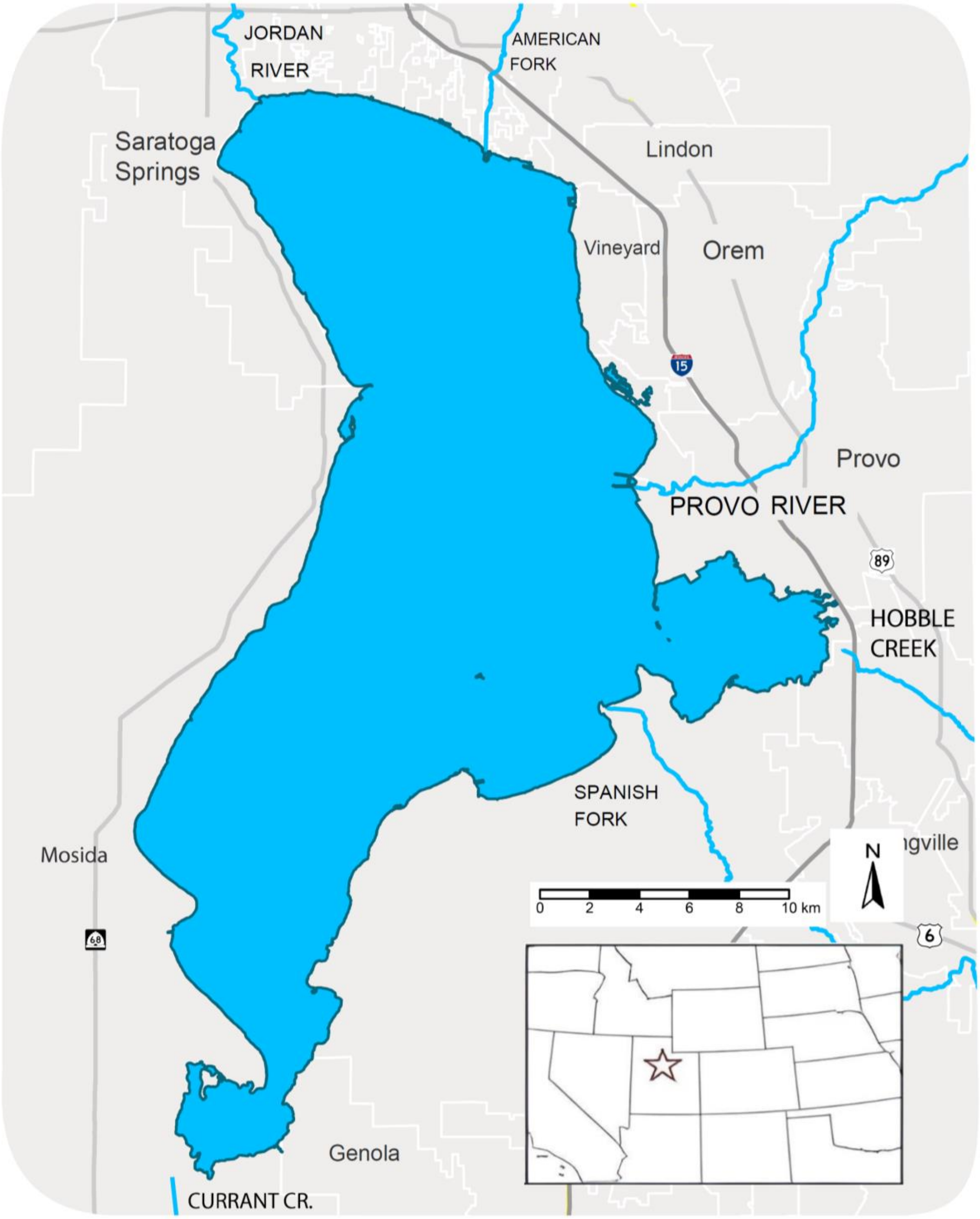

Figure III-1. Map of Utah Lake.

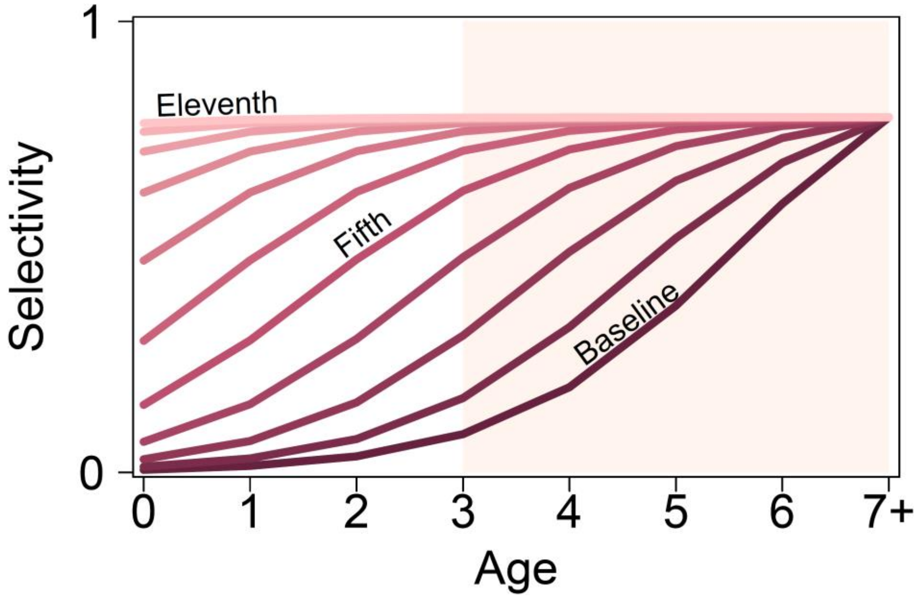

Figure III-2. 11 selectivity scenarios. The darkest, right-most curve is the baseline selectivity obtained from the large mesh gear selectivity analysis and the left-most curve is the 11th scenario. The baseline, fifth, and eleventh scenario are labeled. The shaded region represents the adult age classes.

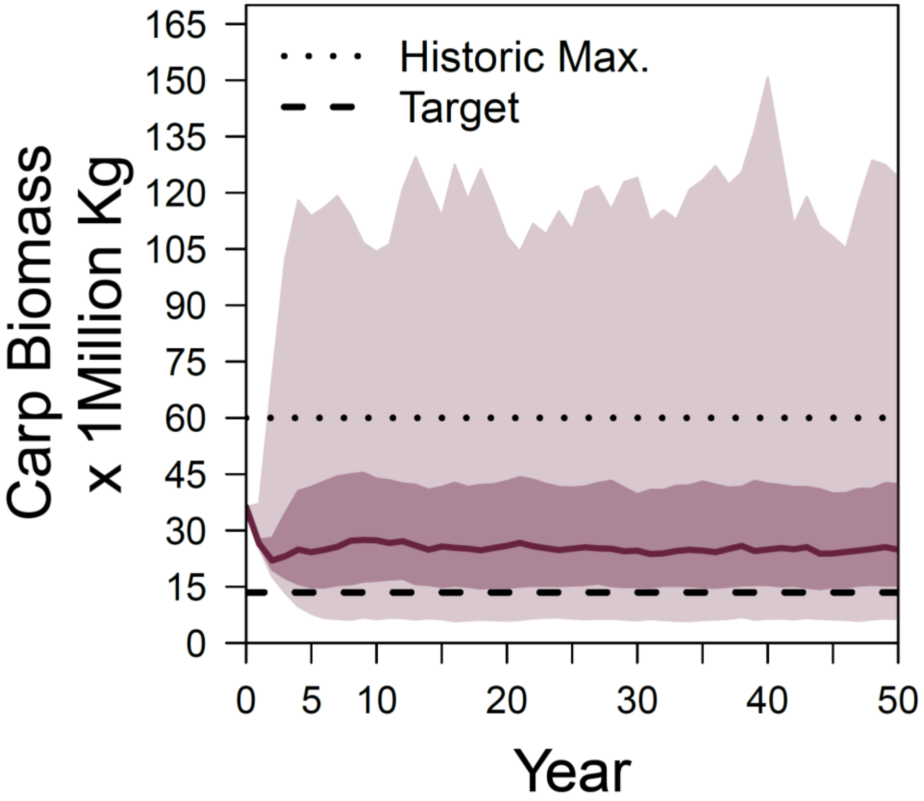

Figure III-3. Simulated carp biomass given current gear selectivity and maximum historic effort. The maroon line shows the median model estimate, while the dark and light shaded regions show the 50% and 95% confidence intervals, respectively. The dashed line is the target biomass (25% of the maximum historic biomass, shown with the dotted line).

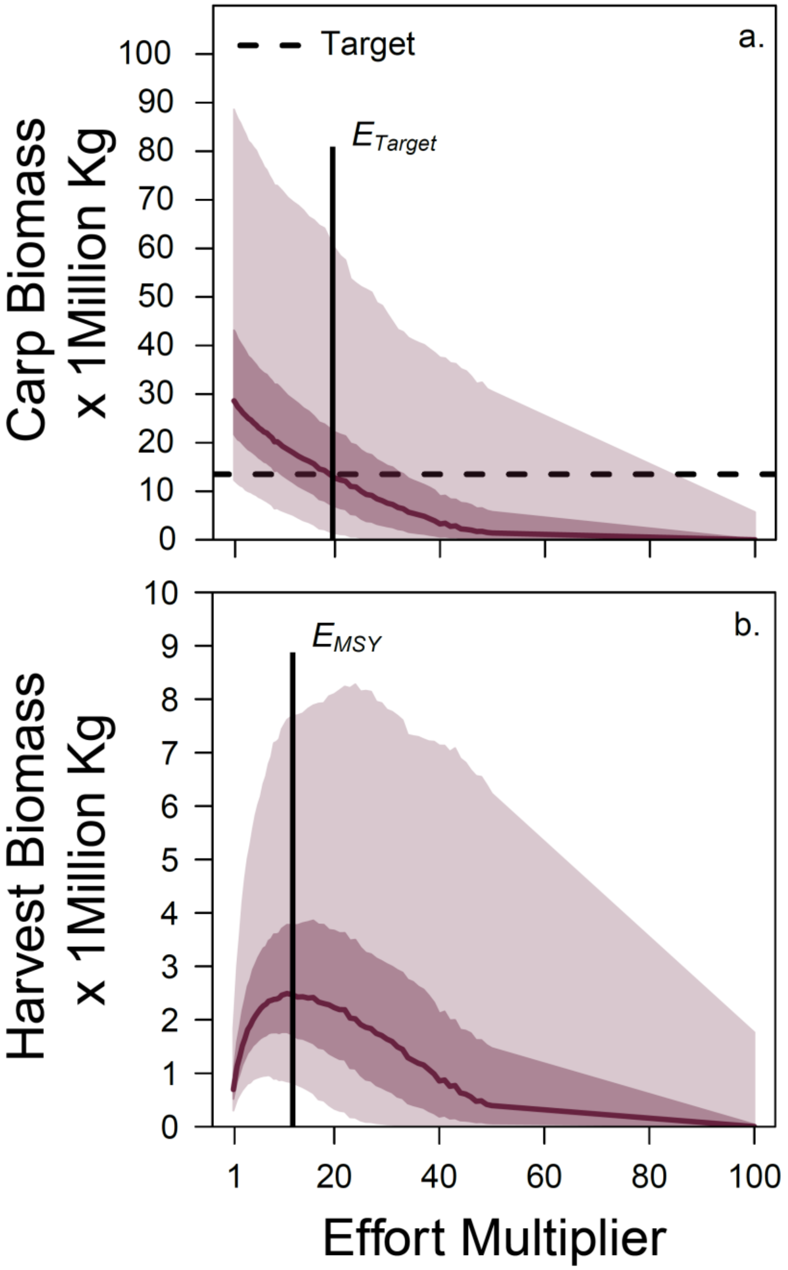

Figure III-4. Estimated average carp biomass (a) and harvest (b) given baseline selectivity across increasing levels of effort. The maroon line is the median model estimate while the dark and light shaded regions are the 50% and 95% confidence intervals. The dashed line is the target biomass (25% of the maximum historic biomass.

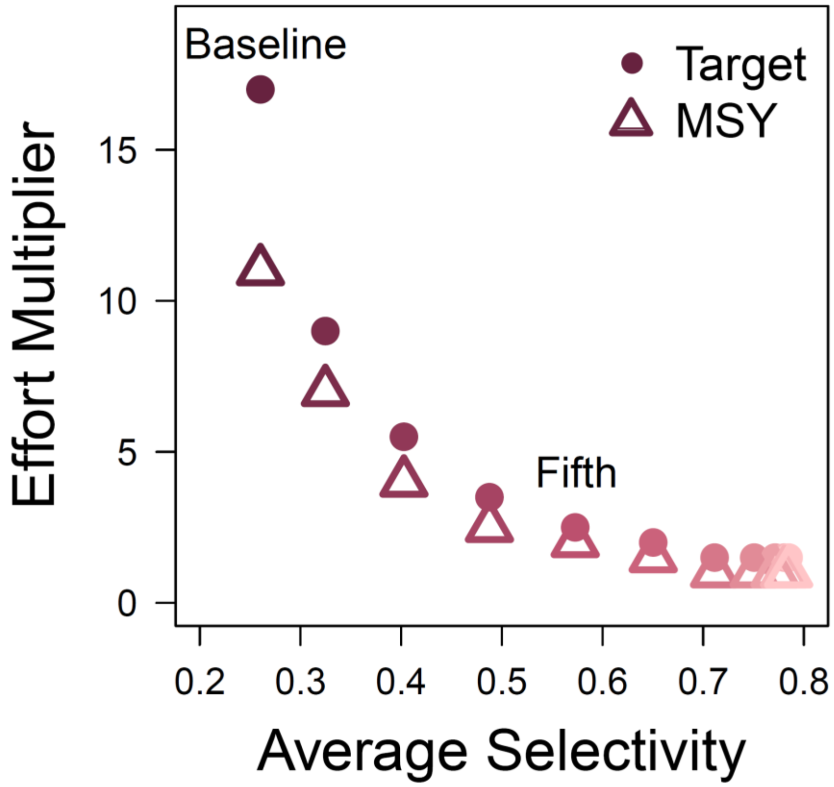

Figure III-5. Effort required to reach 75% reduction target (E_{Target}, circle) or MSY (E_{MSY}, triangle). Color relates to the selectivity curves in Fig. 2 and the baseline and fifth selectivity scenarios are labeled. For the baseline selectivity scenario, the points represent the vertical lines denoting E_{Target} and E_{MSY} on Fig. 4.

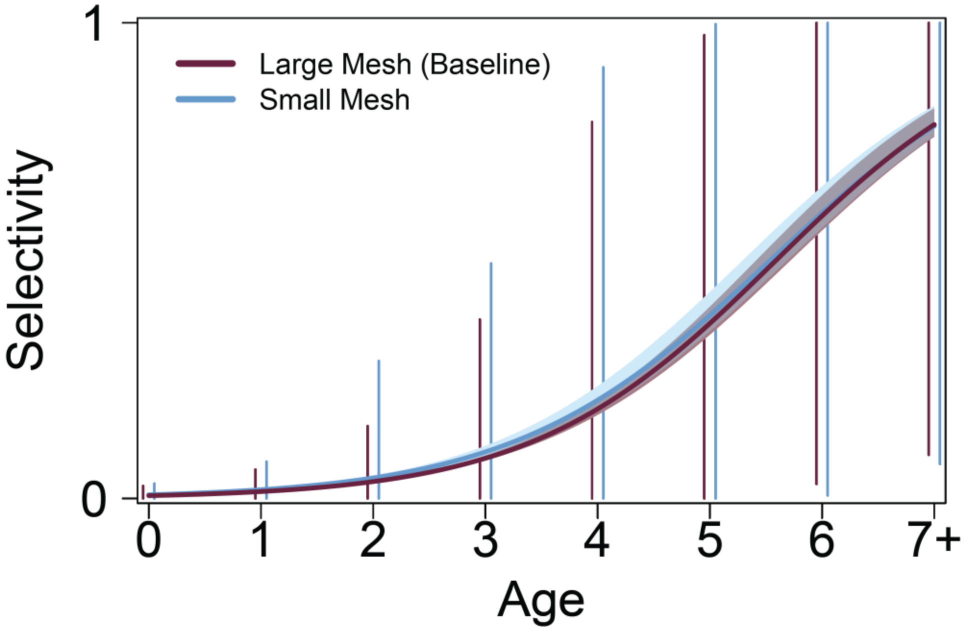

Figure S1. Comparison of large and small mesh seine selectivity. The maroon and blue curves represent the large and small mesh median model estimates while the shaded region represents the 95% confidence interval of the logistic curve. The vertical lines show the 95% confidence interval for each age's selectivity beta distribution.

Table S1. Breakdown of all simulated effort levels.

Starting effort metric	**Ending effort metric**	**Increment of increase between metrics**	**Number of effort levels**
Historic mean	Historic maximum	Historic maximum – historic mean	2
1.5x historic maximum	10x historic maximum	0.5x historic maximum	18
11x historic maximum	49x historic maximum	Historic maximum	39
50x historic maximum	100x historic maximum	50x historic maximum	2

CHAPTER IV

CONCLUSIONS

Managers globally seek to mitigate the negative effects of invasive species through population control (Green & Grosholz, 2021; Mack et al., 2000), as invasive species represent one of the greatest threats to global biodiversity (Doherty et al., 2016; Reid et al., 2005). However, the success of control efforts varies greatly and typically requires a long-term, ecosystem-based approach (Myers et al., 2000; Simberloff, 2003). Biological characteristics and density-dependent population processes often contribute to population resilience and complicate control efforts (Grosholz et al., 2021; Zipkin et al., 2009). In freshwater systems, the interconnectedness of waterways makes reintroductions likely (Rytwinski et al., 2018), and the underwater nature of study subjects makes detection difficult, further complicating control efforts. Although the Utah Lake common carp (*Cyprinus carpio*; hereafter "carp") control program likely got close to achieving the target biomass in 2017, the population has since increased in part due to the selectivity of removal gears and subsequent compensatory recruitment (Walsworth et al., 2020; Walsworth et al., 2023). My research provides insights into the detection and capture of these cryptic younger age classes and the determination of which age classes confer the most benefit when targeted.

My work centered around the idea of influencing selectivity, the proportion of fish at a given size that are captured with a removal gear (Millar & Fryer, 1999), via the identification of fishing gears or methods that improve selectivity of cryptic age classes and identifying which age classes confer the most benefit when their selectivity is increased. Selectivity has long been discussed in commercial fisheries (e.g. Beverton &

Holt, 1957; Hilborn & Walters, 1992), and researchers have urged for it to be included in management frameworks because of the impact it can have on population demographics and sustainable harvest (Vasilakopoulos et al., 2020). Selectivity can be impacted by the physical characteristics of a fishing gear and the location or timing of fishing (Millar & Fryer, 1999; Sampson & Scott, 2012), and I aimed to incorporate these dimensions into my field study. Because there are a limited number of scenarios that can be tested in the real world, I additionally used a simulation framework to evaluate the impact of gear selectivity on control efficacy. By combining field data and simulation modeling, I was able to address both the immediate need and long-term implications of selectivity on the Utah Lake carp control program.

The first chapter of this thesis centered around a lake-wide field survey of 16 perimeter sites sampled between 2021 and 2023. The objectives of this field survey were to 1) identify a gear that could target juvenile and small adult carp in Utah Lake and 2) characterize the spatio-temporal distribution of juvenile and small adult carp in Utah Lake. For my first objective, I was able to identify trap nets as the gear that could most effectively target these cryptic age classes. However, trap net performance was still limited, and it would be difficult to implement on the scale necessary to be impactful in the control efforts. In regard to my second objective, I was able to identify temporal catch patterns that align with the life-history characteristics of different age classes. While this reinforces the idea that the different life history strategies of each age class must be considered when developing harvest plans, my results were likely limited by low catch of these cryptic age classes. Additional fieldwork may further elucidate spatio-temporal patterns that could inform future control efforts. However, it is also important to consider which age classes of carp are important to target, as it may not be necessary to target all age classes.

The second chapter of this thesis revolved around the development of a simulation framework for evaluating the impact of selectivity on control efficacy. The objectives of this chapter were to (1) assess how control efficacy improves with increased selectivity of younger age classes and (2) identify the age-classes that provide the greatest control benefit when targeted. I was able to show that small improvements in selectivity initially resulted in drastic reductions in the amount of effort required to achieve control targets, but that diminishing returns limited the effects of further improving selectivity. I identified the importance of targeting all adult age classes and found that additionally targeting juvenile age classes conferred minimal benefit. While I have not identified a gear that exhibits improved selectivity, control efforts can focus on improving adult selectivity, but do not necessarily need to worry about targeting all age classes. This can additionally inform future field experiments, which may benefit from focusing on identifying fishing methods that target these cryptic young adult age classes. I also found that regardless of selectivity, the Utah Lake carp control program has historically fished at a sustainable rate. This means that successfully controlling the Utah Lake carp population likely requires both improving younger adult gear selectivity and increasing the level of fishing effort.

Acknowledging that successful control likely requires great, sustained effort is an important aspect of achieving invasive species control. Initial reports for the Utah Lake carp control program provided a rough timeline that suggested the 75% target could be achieved within five years and that once the target was achieved, the required harvest would be substantially decreased (SWCA, 2002, 2005, 2006). While my simulation framework shows that this 75% reduction target does likely result in a smaller biomass of fish being captured once the target is achieved, it also makes it clear that achieving and sustaining this level of biomass requires greater effort than has ever been recorded in Utah Lake. By incorporating sustainable harvest metrics traditionally used in commercial fisheries management, I am able to provide insights into the long-term implications of harvest management. Managers in Utah Lake and elsewhere have limited budgets in order to achieve their management targets, and it is important to have a realistic idea of the level of investment required for successful control.

As invasive species continue to proliferate and management programs struggle to control invaders, it is critical that we evaluate the feasibility of management objectives. It has long been acknowledged that eradication is a lofty, difficult goal to achieve (Myers et al., 2000; Rejmánek & Pitcairn, 2002; Simberloff, 2003) and while control efforts are often seen as more feasible, their success is uncertain and requires sustained effort (Rytwinski et al., 2018; Yick et al., 2021). It is important to consider the implications of life history, density dependence, and gear selectivity in feasibility assessments to avoid investing in programs that are later deemed infeasible and abandoned. Scientific management tools including annual monitoring, targeted field surveys, and simulation modeling can be used together to help managers assess the likelihood of success earlier in the management process. Evaluating the feasibility of management objectives is a critical step in determining where investments will have the most impact and ultimately allows managers to more efficiently allocate their limited resources.

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