



Modeling control of Common Carp (*Cyprinus carpio*) in a shallow lake–wetland system

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Abstract The introduction of Common Carp (*Cyprinus carpio*) into North American waterways has led to widespread alteration of aquatic ecosystems. Control of this invader has proven extremely difficult due to its capacity for rapid population growth. To help understand how Common Carp can potentially be controlled we developed a population dynamics model (CarpMOD) to explore the efficacy of active and passive control measures that impose mortality on multiple life stages (embryos, juveniles and adults). We applied CarpMOD to Common Carp in Malheur Lake, a large shallow lake in Southeast Oregon, USA. Simulated control measures included commercial harvest of adults, trapping of juveniles, embryo electroshocking, and passive removal imposed via avian predation.

Results from CarpMOD suggest that no single active removal method would decrease Common Carp biomass below the targeted 50 kg/ha threshold. Combinations of two or all three active removal methods could, however, reduce biomass below the desired threshold due to cumulative mortality on multiple life stages. CarpMOD simulations suggest that the level of carp removal necessary to reach the desired biomass threshold is approximately 40% at each life-stage, which may be unrealistic to maintain over longer time scales. Passive removal via avian predation may also contribute to suppression of Common Carp, but was not sufficient in isolation to reduce biomass below the desired threshold. Collectively, our results indicate control of Common Carp as a sole means of ecosystem restoration is unlikely to be effective in the system we modeled. This suggests additional means of restoration may be warranted, perhaps in combination with control of Common Carp, or development of more effective control measures.

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Introduction

Shallow lakes and wetland ecosystems are among some of the most important habitats on Earth due to their numerous ecological functions, such as ground-water recharge, water purification, flood protection, and habitat for a varied collection of aquatic and terrestrial species (Jeppesen et al. 1997). These ecosystems frequently exist in two alternative states (clear or turbid), with the clear state defined by the presence of aquatic macrophytes and zooplankton, as well as low water column nutrients, and decreased phytoplankton biomass, whereas the turbid state is defined by the opposite (Scheffer 1990, 1993; Güneralp and Barlas 2003). A shift from a clear to a turbid state can be induced by several factors (e.g., climatic change, loading of nutrients), and these same factors can increase the system's resistance to a shift back to the clear state (Güneralp and Barlas 2003; Hargeby et al. 2004). Nonnative species, in particular, have been shown to facilitate shifts in water clarity in wetland and lake ecosystems, with cascading effects on ecosystem services (Van Duin et al. 2001; Scheffer et al. 2001).

In the United States, approximately 50,000 nonnative species have established populations outside of their natural range, causing an estimated \$120 billion in environmental damages each year (Pimentel et al. 2005). Many of these species were introduced deliberately, such as the Common Carp (*Cyprinus carpio*), which were distributed by the US Fish Commission throughout the United States to serve as an alternative food source for rural Americans from 1889–1897 ($\approx$ 2.4 million individual carp; Smiley 1886, 1896; Cole 1905; Nico and Fuller 1999). The Common Carp (hereafter “carp”) is the eighth most prevalent nonnative invader in the world (Lowe et al. 2000), often reaching high levels of abundance (> 1000 kg/ha) due to their ability to tolerate a range of abiotic conditions (Bajer et al. 2009; Weber and Brown 2009; Bajer and Sorensen 2010; Bajer et al. 2011).

Once a population of carp becomes established, their activity and mode of feeding can degrade aquatic ecosystems (Koehn 2004; Kloskowski 2011; Pietsch and Hirsch 2015). Benthic foraging uproots aquatic vegetation while simultaneously suspending sediment in the water column, which increases turbidity and diminishes light penetration (Weber and Brown 2009). In turn, this can further inhibit growth and recruitment

of aquatic vegetation (Weber et al. 2011). This positive feedback process can transform shallow lakes from a clear state to a highly turbid state (Bajer et al. 2009; Vilizzi et al. 2015). Carp biomass must be substantially decreased to reduce these impacts and return the aquatic ecosystem to previous conditions (Bajer et al. 2009). Control of carp can be extremely difficult, however, due to their high capacity for population growth and expansion, survival in habitat refugia, and ability to modify their environment to their own advantage (Brown and Walker 2004).

Carp populations exhibit compensatory density dependence (Weber et al. 2016), in which demographic rates (i.e. mortality and recruitment) shift in response to variation in the population's overall density (Rose et al. 2001). Thus, even if carp are removed in large numbers, the species can rebound quickly (biomass doubling time of 2.7 years; Colvin et al. 2012b). Although it is known that carp populations are generally resilient to a wide range of perturbations, predicting the specific effects of alternative control measures is difficult because there are many processes in play. This complexity has led researchers to develop population models to evaluate carp control measures prior to their implementation (Weber and Brown 2009; Bajer et al. 2015).

Modeling has performed a crucial role in the advancement of carp control due to the ability to quickly and effectively investigate alternative control measures (e.g., commercial harvest, separation cages, cyprinid herpesvirus, daughterless carp, pheromone lures, and spawning sabotage). These modeling efforts suggest that successful carp control may require control strategies that target multiple life stages (Brown and Walker 2004; Weber and Brown 2009; Colvin et al. 2012b; Brown and Gilligan 2014; Bajer et al. 2015). For example, a previous modeling project determined that commercial harvest was unsuccessful when targeting one life stage (adults), however the targeting of two or more life stages (adults and juveniles) resulted in a reduction of carp below the target biomass (< 100 kg/ha; Lechelt and Bajer 2016).

Although imposing mortality on two or more life stages of carp can hypothetically result in effective control, in practice, carp control is challenging because most of the developed removal methods are focused on adults (Weber et al. 2011), with minimal impact on other life stages (e.g., embryo to juvenile). Thus, there is not only a need to identify new removal

methods that target juvenile carp and carp embryos (Carl et al. 2016; Simpson et al. 2018; Poole et al. 2018), but also to examine how these novel approaches perform in combination with adult removal methods. To address this issue, we evaluated four different control measures that span three distinct life-stages and represent both active and passive removal methods: (1) commercial harvest of adults (active), (2) embryo electroshocking of larvae in spawning areas (active), (3) trapping of juveniles via fyke nets (active), and (4) increased avian predation of juveniles (passive).

Additional consideration of avian predation and embryo electroshocking into a model of carp control is important because both have been suggested as a means of control (Coleman et al. 2013; Nutile et al. 2013), but have not been investigated. Avian predation is generally imposed in models implicitly through the Ricker Recruitment function (Ricker 1954; Brown and Gilligan 2014), but here we consider it explicitly. Numerous empirical studies have demonstrated that avian piscivores can have a significant impact on fish populations (Birt et al. 1987), and thus could have major implications for carp control. For instance, both Yellow Perch (*Perca flavescens*) and Smallmouth Bass (*Micropterus dolomieu*) populations were significantly reduced by Double-crested cormorant (*Phalacrocorax auritus*) colonies in Lake Ontario (Burnett et al. 2002; Lantry et al. 2002; Johnson et al. 2015). Avian piscivore populations can be increased in locations with abundant prey by enhancing available nesting habitat (e.g., on islands; Roby et al. 2002). Embryo electroshocking has also been suggested as a control measure for carp because fish embryos are sensitive to electricity prior to the pigmentation stage of development (Warga and Kimmel 1990; Dwyer et al. 1993, 1995; Bohl et al. 2010; Simpson et al. 2018). Furthermore, recent studies have demonstrated that embryo electroshocking can cause a significant decrease in the survival of species closely related to carp (family: *Cyprinidae*), including Fathead Minnow (*Pimephales promelas*) and Zebrafish (*Danio rerio*) when exposed to voltage gradients ≥ 20 V/cm as well as Goldfish (*Carassius auratus*) when exposed to ≥ 16 V/cm (Nutile et al. 2013).

Our overall objective was to develop and apply a model to evaluate conventional means of carp control (e.g., mortality imposed on adults) in the context of interactive effects of mortality on juvenile (e.g., as

imposed by avian predation or juvenile trapping) and larval (e.g., as imposed by embryo electroshocking) life stages. We applied this model to Malheur Lake (Oregon, USA), a large lake–wetland ecosystem with a 65-year legacy of efforts to control invasive carp (Ivey et al. 1998). Specifically, we simulated the individual and interactive effects of adult commercial harvest, embryo electroshocking, juvenile trapping, and the individual effects of bird predation on carp population dynamics. Results of this effort provide novel insights into interactions among multiple factors that drive the success or failure of carp control within lakes and associated wetlands.

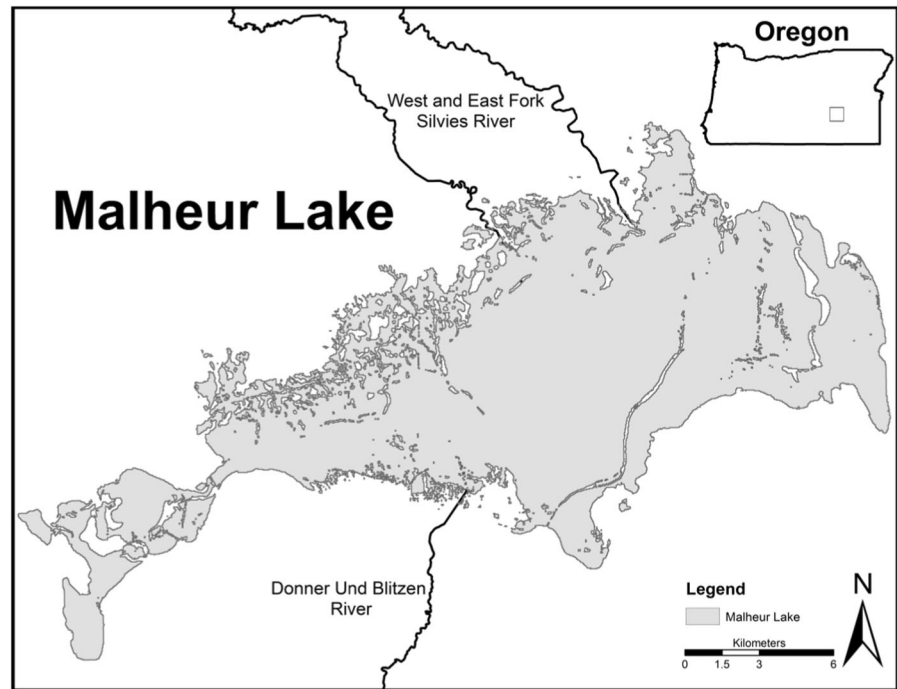
Methods

Study area

The case study system for our model analysis was Malheur Lake (elev. = 1255.17 m; Fig. 1), located in Southeastern Oregon (Lat: 43.3115 and Long: -118.7952) within the Malheur National Wildlife Refuge (MNWR), managed by U.S. Fish and Wildlife Service (USFWS). Malheur Lake is a large (average $\approx 14,000$ ha), shallow (average depth ≈ 0.76 m; max depth ≈ 1.52 m), terminal lake (endorheic basin) with two major freshwater inputs, the Silvies and Donner und Blitzen rivers, with discharges that are primarily snowmelt driven and drain a total area of ≈ 7770 km² (Miller 2012; Williams et al. 2014). During the period 1975–2009 the mean annual precipitation was 27.94 cm and the mean annual temperature was 7.94 °C with July being the warmest month (mean: 26.39 °C) and January as the coldest month (mean: -7.56 °C; Williams et al. 2014).

Malheur Lake was once one of the largest freshwater hemi-marshes in North America, and served as an important transitional area for migratory ducks and geese (Duebbert 1969; Cornely 1982; MNWR 2012). President Theodore Roosevelt established the MNWR in 1908 to preserve habitat for migratory birds and the breeding grounds of other native bird species. Historically Malheur Lake was predominantly a hardstem bulrush marsh (*Scirpus acutu*) with interspersed open zones from shore to shore. Emergent vegetation dominated the shallow areas (0–0.5 m) with hardstem bulrush, broad-fruited burreed (*Sparganium eurycarpum*), common cattail (*Typha latifolia*), baltic rush

Fig. 1 Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The gray shaded region depicts the long-term average lake area ($\approx 14,000$ ha)



(*Juncus balticus*), and sedges (*Carex* spp.) being the most common. The deepest areas of the lake (0.5–1.5 m), which are more permanently flooded, consist of open water with submergent vegetation such as water milfoil (*Myriophyllum exalbescens*), horned pondweed (*Zannichellia palustris*), and sago pondweed (*Stuckenia pectinate*; Duebbert 1969).

In the 1920s nonnative carp were introduced into the Silves River and by the early 1950s large numbers of carp were observed in Malheur Lake (Ivey et al. 1998). An immediate decline in water quality, waterfowl productivity, and aquatic vegetation was detected. Most notably, by 1955 the once abundant sago pondweed (*Potamogeton pectinatus*) had completely disappeared, followed by a subsequent decline in waterfowl such as the Canvasback duck (*Aythya valisineria*) that thrive on the sago pondweed (Erickson 1948; Ivey et al. 1998). Over the past 65 years, biologists at MNWR have been attempting to control the population of carp in Malheur Lake to restore the aquatic ecosystem back to pre-invasion conditions (Ivey et al. 1998). Several large-scale carp removal efforts have been conducted, including eight rotenone (piscicide) treatments. Studies conducted in the years following the rotenone treatments determined that both aquatic vegetation and waterfowl production

rebounded significantly. However, the rotenone treatments never succeeded in completely eradicating carp because of their ability to survive in refugia habitats (i.e. shallow wetlands and the surrounding watersheds), which enabled their eventual reestablishment, returning the ecosystem to conditions dominated by poor water quality, drastically reduced aquatic vegetation, and lowered waterfowl productivity (Ivey et al. 1998).

Carp population model

The carp population model (CarpMOD) was constructed in STELLA 10.0.6 (ISEE Systems, Inc. Lebanon, NH USA¹), and is a modified version of CarpSIM (Brown and Walker 2004; Brown and Gilligan 2014). The major differences between CarpSIM and CarpMOD is the inclusion of: (1) density-dependent mortality for all carp age classes, and (2) predation on juvenile carp by avian piscivores. Juvenile carp recruit into CarpMOD after completing their first year of life (age 1), whereby recruitment

¹ Use of trade or firm names is for descriptive purposes only and does not constitute endorsement of any product or service by the U.S. Government.

success is based on a density-dependent recruitment relationship between the density (ha^{-1}) of spawning adults and the subsequent juvenile recruits (age 0; Fig. 2; Ricker 1954; Harris and Gehrke 1997; Koehn et al. 2000; Brown and Walker 2004). Successful recruits are then tracked by age, from age 1 to age 20. For each age class, the strength of natural density dependent mortality is a function of carp length; i.e., smaller carp experience higher density dependent mortality than larger carp (Charnov et al. 2013; Bajer et al. 2015). In addition, mortality of juvenile carp (< age 4) is increased due to avian predation as a function of the population size and annual consumption rates of avian piscivores (Appendix 1; Wiens and Scott 1975; Roby et al. 2003). Carp that survive these natural sources of mortality increase in length and

weight each year according to a Von Bertalanffy Growth Model (VBGM) and a standard length–weight relationship, respectively (Von Bertalanffy 1938; Anderson and Neumann 1996; Schneider et al. 2000; Jackson et al. 2008). Further description of the major equations used in CarpMOD are presented in Appendix 1. Linking these processes together, the carp population goes through an exponential growth phase until the population meets and surpasses the lakes carrying capacity, then density-dependent mortality forces the population to decrease back towards the equilibrium carrying capacity. CarpMOD is a non-sex specific, discrete, deterministic model (outputs determined by initial parameter values), executed on an annual time step ($\text{DT} = 1$) using Euler's numerical

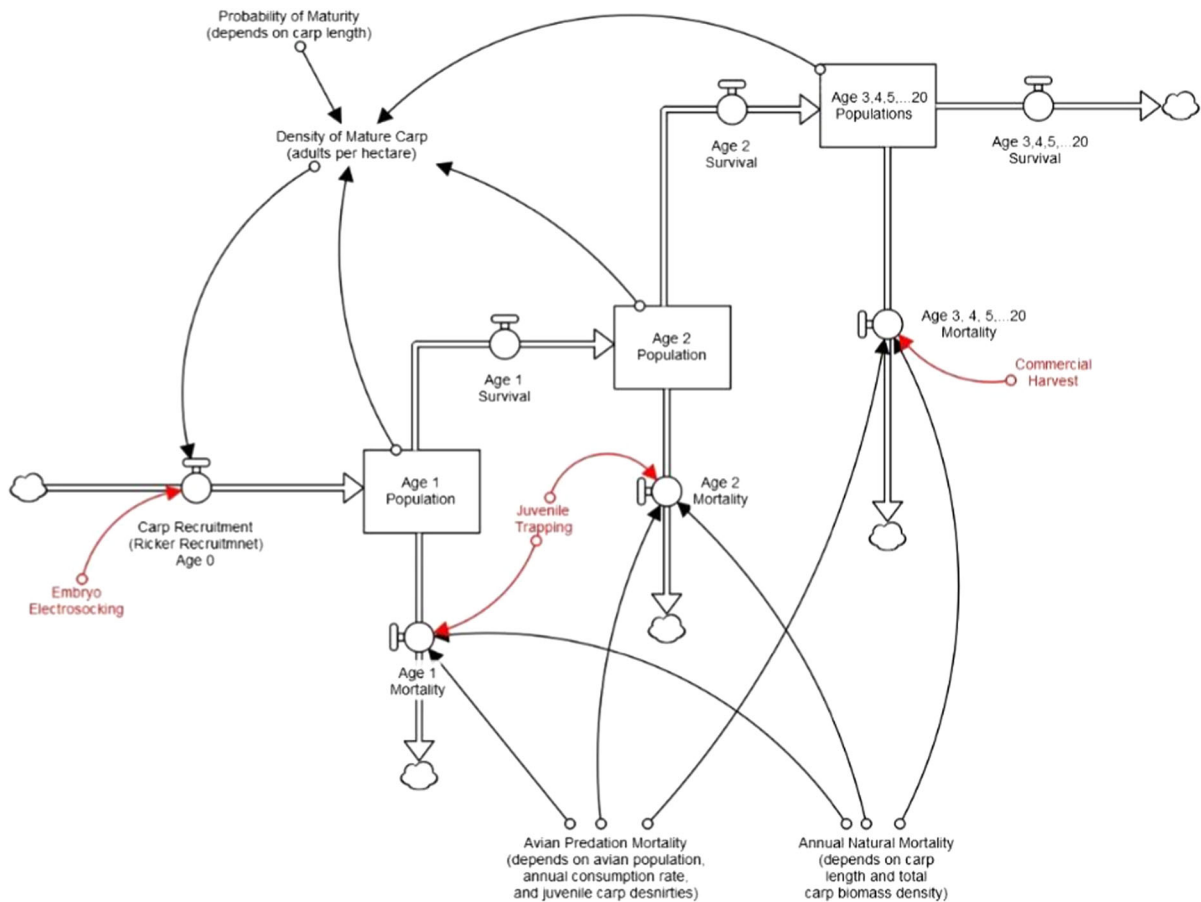


Fig. 2 Conceptual Model of the carp population model. Boxes represent stocks of carp in each age class (from age 1 to age 20); valves (white arrows) depict flow of carp from one age to the next, recruitment, and mortality; small black arrows denote

causal relationships between model components; and small red arrows represent active control measure imposed on the carp population. (Color figure online)

Table 1 Equations used in CarpMOD to simulate the population dynamics of carp in Malheur Lake

Model component	Equation	References
Von Bertalanffy growth model (VBGM)	$L_{(A)} = L_{\infty} (1 - e^{-k(A-t_0)})$	Von Bertalanffy (1938)
Length to weight	$W = aL^b$	Schneider et al. (2000)
Probability of maturity	$\rho_i = \left(1 + e^{\ln(19)(L_{(A)} - LM50)/(LM50 - LM95)}\right)^{-1}$	Brown and Walker (2004)
Ricker recruitment	$R = a * S * \exp(-\beta * S)$	Ricker (1954), Brown and Walker (2004)
Annual natural mortality	$V_{(A)} = 1 - e^{-0.006 \left(\frac{L_{(A)}}{L_{\infty}}\right)^{-1.5} + 10^{-4} \cdot D}$	Charnov et al. (2013), Bajer et al. (2015)

integration method, initiated with 500 age 1 carp, and ran for 100 years.

The five major equations used in CarpMOD are displayed in Table 1² and are based on previously published studies. Growth in length (mm) is simulated via the VBGM, where $L_{(A)}$ is the length of carp at age, L_{∞} is theoretical maximum length, k is the growth coefficient, and t_0 is the theoretical length of the carp at age zero (Von Bertalanffy 1938). The weight-to-length equation relates carp length (L) to weight (W) at each age class using a simple exponential model, where a and b are constant coefficient and exponent values, respectively (Schneider et al. 2000). Maturity is simulated via a probability of maturity equation, where ρ_i is the probability of maturity and LM50/LM95 are the length (mm) in which 50% and 95% of

the carp population is mature respectively (Brown et al. 2003). Annual recruitment is simulated via the Ricker Recruitment equation and consists of the total annual recruits per hectare (R), the numbers of mature individuals per hectare (S), a density-independent coefficient (α), and a density-dependent coefficient (β) and is recalculated at each progressive time step (Ricker 1954). Annual density dependent mortality is simulated via the annual natural mortality equation, where $V_{(A)}$ is the annual mortality of carp at age and D is the density of age 1 + carp (kg/ha), which is recalculated every time step as carp density changes (Charnov et al. 2013; Bajer et al. 2015). A bioenergetics approach was used to estimate the annual consumption of carp by three native avian piscivores: Double-crested Cormorant (*Phalacrocorax auritus*), American White Pelican (*Pelecanus erythrorhynchos*), and Caspian Tern (*Hydroprogne caspia*). The details of the avian predation component of the model are presented in Appendix 2 (Wiens and Scott 1975; Roby et al. 2003).

Sensitivity analysis

A global sensitivity analysis (GSA) of CarpMOD was conducted to investigate how uncertainty in the value of model parameters influences simulated carp biomass (Loucks et al. 2005). In the GSA we ran 10,000 separate model simulations, we randomly selected values of the nine major model parameters (parameters in which uncertainties existed), and we maintained these randomly selected model parameter values throughout the 100 year simulation (Table 2). For each simulation, the values for each parameter

² Table 1. The Von Bertalanffy's growth model (VBGM) equation consists of $L_{(A)}$ which is the length of the carp at age, L_{∞} is theoretical maximum length, k is the growth coefficient, and t_0 is the theoretical length of the carp at age zero (Von Bertalanffy 1938). The Length to Weight equation consists of W which is the weight (g), a and b which are constants estimated via regression analysis (Schneider et al. 2000). The Probability of Maturity equation consists of ρ_i which is the probability of maturity, $L_{(A)}$ is the length at age, LM50 is the length (mm) at 50% maturity, and LM95 is the length (mm) at 95% maturity (Brown et al. 2003). The Ricker Recruitment Model consists of R which is the total annual recruits per hectare, S is the numbers of mature individuals per hectare, α is the density-independent coefficient, β is the density-dependent coefficient, and EE_R is the embryo electroshocking rate (Ricker 1954). The Annual Natural Mortality equations consists of $V_{(A)}$ which is the annual mortality at age A of carp, L is the average length of carp at age A , L_{∞} is the asymptotic average length (mm) of the carp population, D is the density of age-1 + carp (kg/ha), JT_R is the juvenile trapping rate, and CH_R is the commercial harvest rate (Charnov et al. 2013; Bajer et al. 2015).

Table 2 Values of CarpMOD parameters included in the global sensitivity analysis

Parameters	Symbol	Function	Mean	Variance	References
Alpha coefficient	a	W–L	4.531975	0.03952	Derived via data from Malheur Lake
Beta coefficient	b	W–L	2.869073	0.01461	Derived via data from Malheur Lake
Theo. Len. at Age 0	t_0	VBGM	– 0.5482	0.25022	Derived via data from Malheur Lake
Growth coefficient	k	VBGM	0.13327	0.01938	Derived via data from Malheur Lake
Theo. Max Len.	L_∞	VBGM	818.02754	41.3931	Derived via data from Malheur Lake
Alpha coefficient	α	Recruitment	20.0825	16.1242	Brown and Walker (2004), Brown and Gilligan (2014)
Beta coefficient	β	Recruitment	0.0162	0.0039	Brown and Walker (2004), Brown and Gilligan (2014)
Len. of maturity 50	LM50	Maturity	309.667	31.754	Brown and Walker (2004), Brown and Gilligan (2014)
Len. of maturity 95	LM95	Maturity	364.667	47.343	Brown and Walker (2004), Brown and Gilligan (2014)

were selected from a normal distribution, either using data from Malheur Lake, or literature sources (Table 2). The selected parameter values and the associated modeled carp biomass for each of the 10,000 model runs was input into the Random Forest Package (R package Random Forest 4.6-2) using R statistical computing software (R Development Core Team 2017; Breiman and Cutler 2011). The Random Forest Package is a nonparametric classification technique, which employs a random subset of data to generate multiple classification and regression trees (CART). The CART outputs are then used to calculate the residual sum of squared errors (normalized node impurity) for each model parameter to deliver an output of the relative importance for each parameter in determining modeled carp biomass (Breiman and Cutler 2011).

Carp removal scenarios

Active carp control measures involved simulating population responses to commercial harvest of adult carp (> 250 mm; age 3+), embryo electroshocking (represented via decreased recruitment), and trapping of juveniles (ages 1–2). For each active control measure, we simulated responses to multiple levels of removal, from 0 to 100% in 10% intervals. We then simulated the response to simultaneously employing two removal methods, and then all three methods. Again, for each of these combined scenarios, removal levels were increased from 0 to 100% in 10% intervals. Due to a modeled delta time of 1, the active control measures are occurring at the same time as natural mortality.

The active control measures in CarpMOD are aimed at reducing the carp population via pulsed removals at distinct life stages. Embryo electroshocking represents a decrease in the annual recruitment, thus the given embryo electroshocking mortality rate (EE_R) decreases the output of annual recruits from the Ricker Recruitment equations (Ricker 1954; Table 1). Juvenile trapping simulates the removals of carp ages 1 and 2 (≈ 151 and 234 mm respectively), which are not harvested by commercial fishing gear due to gear selectivity, thus the juvenile trapping rate (JT_R) increases the annual natural mortality of carp age 1 and 2 (Table 1). Commercial harvest affects carp age 3 + (Age 3 ≈ 307 mm) due to the gear selectivity (> 250 mm) used by the fishermen, thus commercial harvest rate (CH_R) increases the annual natural mortality of age 3 + carp (Table 1).

Passive carp control involved increasing the populations of avian piscivores, and the associated predation on carp. We considered this to be a “passive” method due to the minimal amount of follow-up necessary after implementation (i.e. construction of avian piscivore nesting habitat). To investigate this passive removal scenario we simulated carp population responses to a doubling and tripling in the abundance of avian piscivores currently at Malheur Lake.

All removal scenarios were implemented in year 70 (10 years after population reaches equilibrium) and run for 30 years, with a lake area of 14,000 ha (Malheur Lake’s historical average) to focus on the interactions within the carp population during removal scenarios. This ensured that increases and decreases in the overall carp biomass were due only to removal

actions, and not influenced by lake fluctuations, which could increase/decrease densities independent of removal actions. Uncertainty in predicted responses to each removal scenario was determined by running a separate sensitivity analysis for each scenario, using the same design as described above for the GSA. In other words, each removal scenario was ran 10,000 times to get 10,000 separate estimates of carp biomass, of which the final simulation year (year 100) was used to construct box-and-whisker plots. Removal scenarios were defined as successful if the median model output of carp biomass was reduced below 50 kg/ha [lower than 112.1 kg/ha specified by MNWR's Comprehensive Conservation Plan: CCP, Comprehensive Conservation Plan (CCP) 2013]³, which is hypothesized to be to the threshold at which waterfowl productivity would increase, via the recovery of lake clarity and aquatic vegetation (Vilizzi et al. 2015).

Results

Background model dynamics and sensitivity

The fully parametrized CarpMOD implemented with no control measures predicted a median overall carp biomass of 375 kg/ha (Fig. 3), in which the standing biomass of mature carp (344 kg/ha) vastly exceeded that of non-mature carp (31 kg/ha). On average the avian piscivores consumed ≈ 5.8 kg/ha of age 1 + (≥ 1 years old) carp annually. Furthermore, the model predicted a natural (density-dependent) mortality rate of ≈ 0.57 for age 1 individuals, which is similar to that reported in other studies (Bajer et al. 2015; Osborne 2012).

Modeled carp biomass was highly sensitive to uncertainty in the parameter values investigated in the global sensitivity analysis; 25 and 75% confidence bounds around the median carp biomass (375 kg/ha) were 501 and 237 kg/ha (GSA; Fig. 3). The GSA identified that three of the nine parameters explained 85.1% of the uncertainty in the predicted carp biomass. Predicted carp biomass was most sensitive to model parameters that controlled density dependent recruitment (α Recruitment Coefficient $\approx 52.0\%$ and β Recruitment Coefficient $\approx 16.8\%$) and the

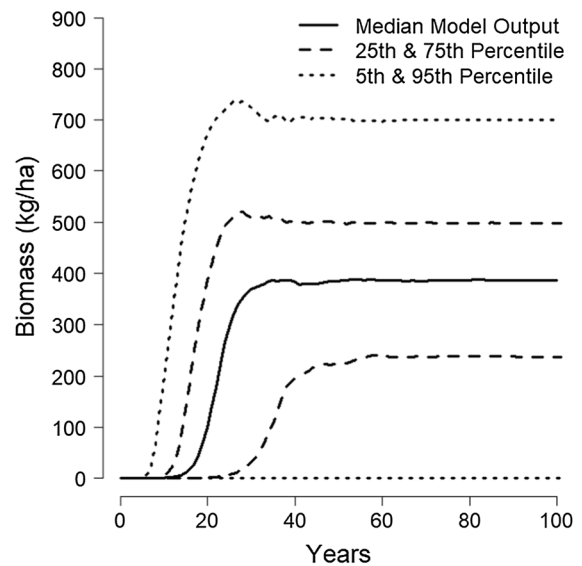


Fig. 3 Modeled dynamics and sensitivity of carp biomass to uncertainty in model parameter values (Table 2). The solid line represents the median modeled outcome and dashed lines represent the 25th and 75th and 5th and 95th percentile bounds from a global sensitivity analysis based on 10,000 simulations (see Methods)

length at age relationship (Growth Coefficient (k) $\approx 16.3\%$; Fig. 4). The relatively large uncertainty attributed to the α Recruitment Coefficient and β Recruitment Coefficient are due, in part, to the large uncertainty in the value of these parameters relative to the other model parameters, as well as their influence on the scale and shape of the stock recruitment (KoeHN et al. 2000; Brown and Walker 2004; Brown and Gilligan 2014; Table 2; Fig. 3). The uncertainties associated with the Growth Coefficient are due to the parameters major influence on length individuals in the population, which directly affects the overall biomass of carp.

Active control scenarios

Although all control methods reduced modeled carp biomass, only combinations of higher levels of commercial harvest and embryo electroshocking (rate $\approx > 0.4$) or combinations of all three removal methods (rate $\approx > 0.3$) could reduce the median predicted carp densities below the desired threshold (< 50 kg/ha; Figs. 5, 6). Due to the collective influences of uncertainties surrounding model parameters (Table 2), however, there were always a few instances

³ Available online: https://www.fws.gov/refuge/Malheur/what_we_do/conservation.html.

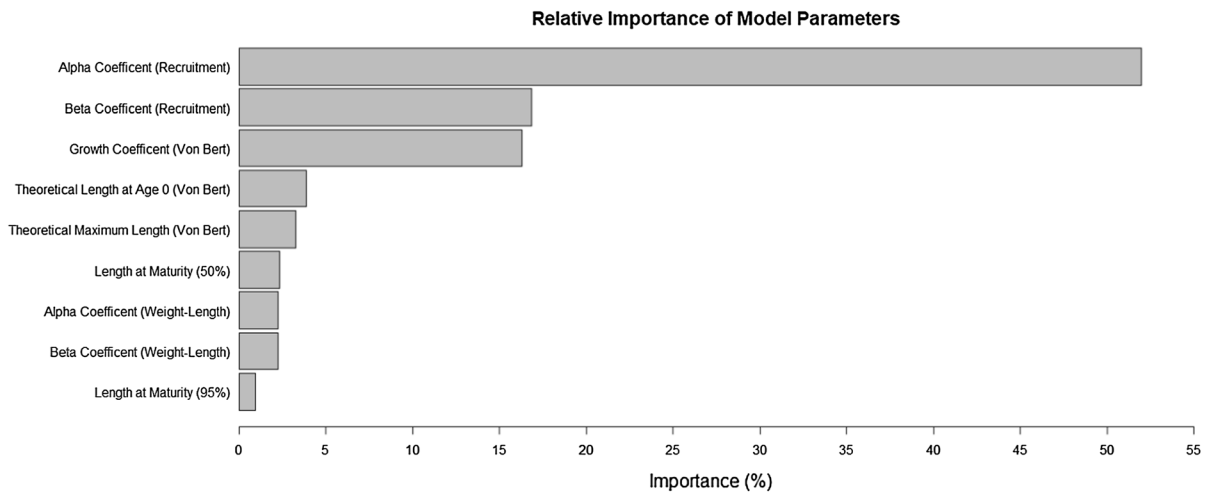


Fig. 4 Relative importance of different model parameters in determining carp biomass from Random Forest analysis (see [Methods](#)), ranked from most important to least important

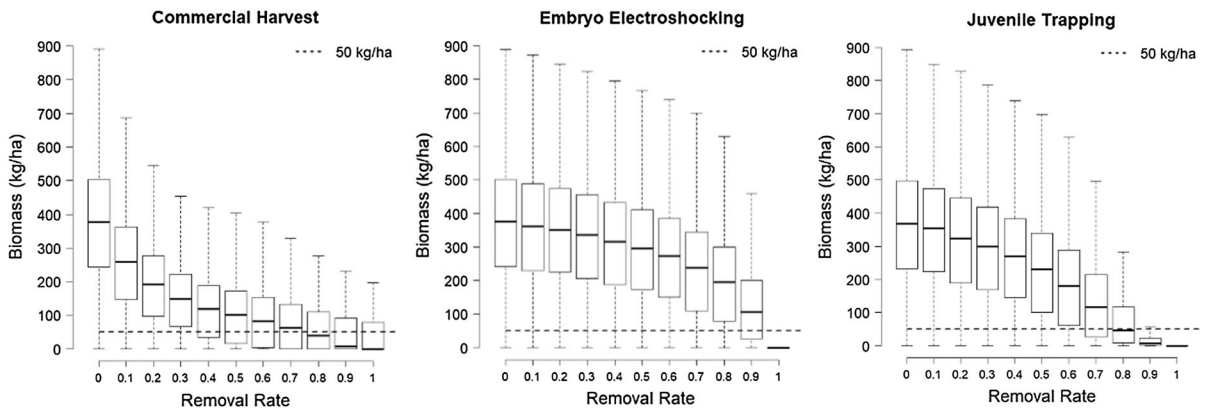


Fig. 5 Modeled carp biomass (kg/ha) resulting from single control methods (commercial harvest (Left), embryo electroshocking (Center), and juvenile trapping (Right)). Box-and-whisker plot were constructed utilizing the final simulated carp biomass (year 100), and demonstrate the sensitivity of modeled

outcomes to uncertainty in model parameter values (see [Methods](#)). The bold black lines within each box are the median outcome, outer edges of box are 0.25 and 0.75 quantiles, and outer whiskers are 0.05 and 0.95 quantiles

where any level of control resulted in a reduction of the carp biomass below the desired threshold (< 50 kg/ha; Figs. 5, 6). However these specific outcomes are highly improbable, and likely represent combinations of model parameters randomly selected in the GSA that are biologically unreasonable (e.g., large variation in recruitment parameters due to a lack of empirical data for our study system).

Passive control scenarios

Similar to active removals, increasing mortality of carp via avian piscivores alone could not reduce carp biomass below the desired management threshold (< 50 kg/ha; Fig. 7). A doubling of the avian piscivore populations led to a reduction of 46 kg/ha in the median carp biomass and a tripling of the populations led to a further reduction of 56 kg/ha.

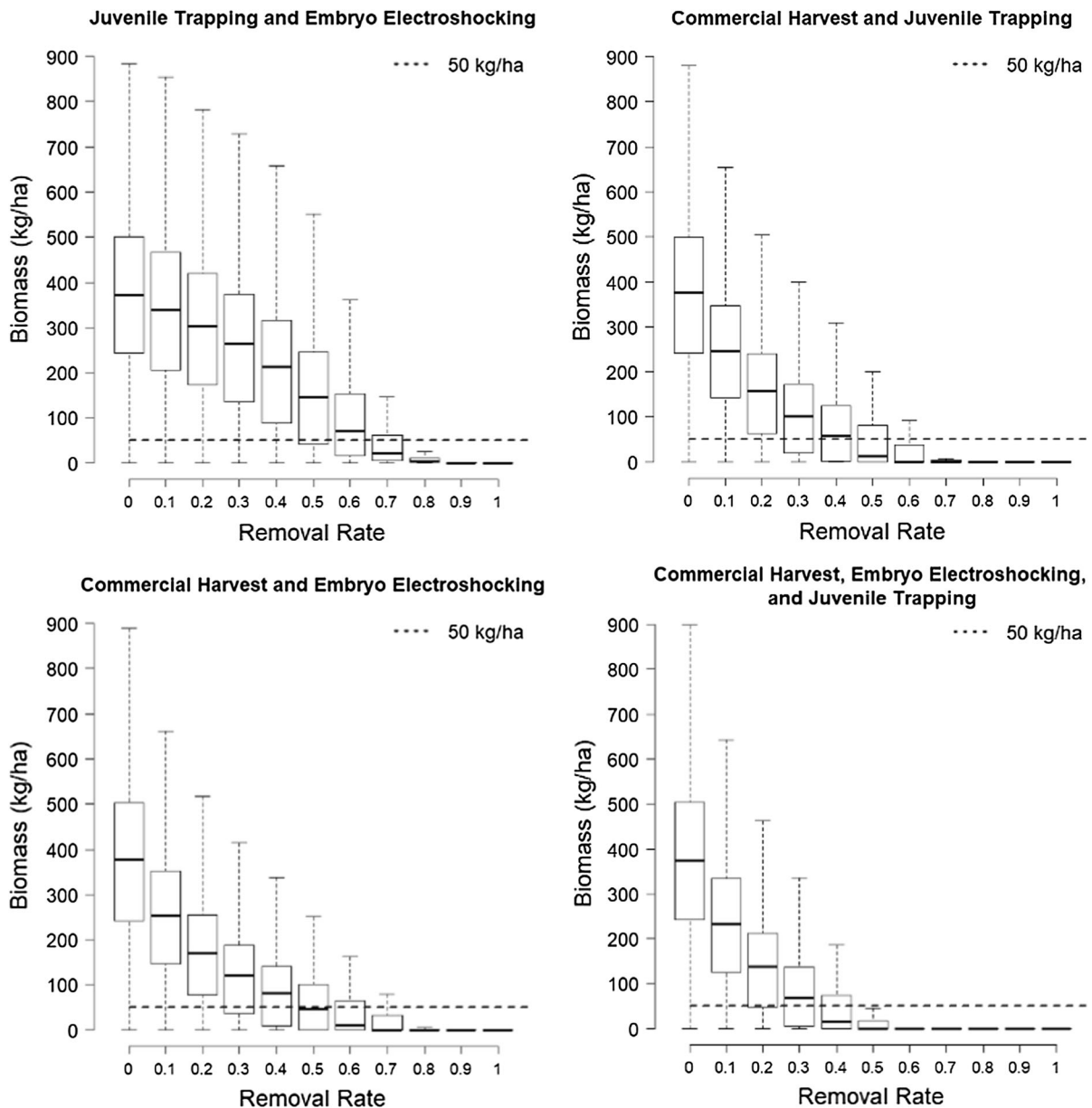


Fig. 6 Results for combinations of control methods [embryo electroshocking and juvenile trapping (top-left), commercial harvest and juvenile trapping (top-right), commercial harvest and embryo electroshocking (bottom-left), and all methods in combination (bottom-right)]. Box-and-whisker plot were constructed utilizing the final simulated carp biomass (year 100),

and demonstrate the sensitivity of modeled outcomes to uncertainty in model parameter values (see [Methods](#)). The bold black lines within each box are the median outcome, outer edges of box are 0.25 and 0.75 quantiles, and outer whiskers are 0.05 and 0.95 quantiles

Discussion

Population models are useful for evaluating control of invasive species because these models can account for complex interactions within the population and

examine alternative control scenarios (Taylor and Hastings 2004; Govindarajulu et al. 2005; Hess et al. 2006; Morris et al. 2011; Caplat et al. 2012). We constructed a carp population model (CarpMOD) to investigate two categories of controls (active and

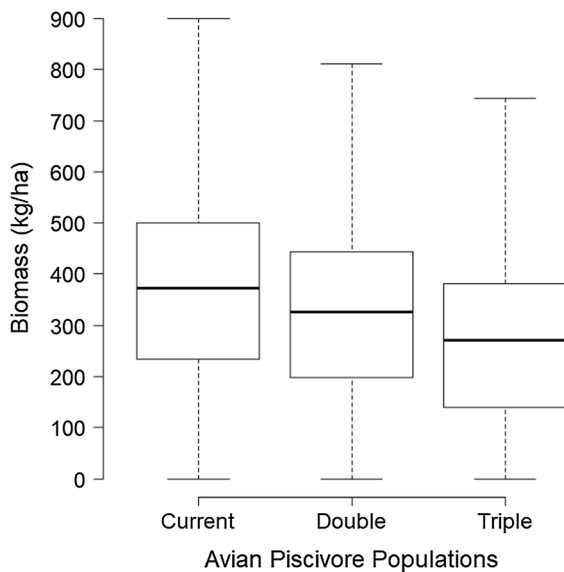


Fig. 7 Simulated biomass (kg/ha) of carp in response to different levels of avian predation (current levels, double current levels, and triple current levels) by three bird species (Double-crested Cormorant, American White Pelican, and Caspian Tern). Box-and-whisker plot show the sensitivity of modeled outcomes to uncertainty in model parameter values (see [Methods](#)). The bold black lines within each box are the median outcome, outer edges of box are 0.25 and 0.75 quantiles, and outer whiskers are 0.05 and 0.95 quantiles

passive), which deliberately targeted multiple life stages. CarpMOD results suggest that no individual control method, active or passive, is likely to decrease carp populations to levels necessary for ecological recovery (< 50 kg/ha; Brown and Walker 2004; Brown and Gilligan 2014; Lechelt and Bajer 2016) in Malheur Lake. However, a combination of intensive application of two (commercial harvest and embryo electroshocking or commercial harvest and juvenile trapping) or all three (commercial harvest, embryo electroshocking, and juvenile trapping) active control methods could potentially reduce carp biomass below presumed ecological recovery thresholds (Fig. 6). In the case of Malheur Lake, these simulations provide a quantitative basis for conducting removal experiments to evaluate whether simulations conform to reality. In practice, however, the high levels of carp removal suggested by the model may be unrealistic to maintain over long time scales.

Targeting the adult life stage of invasive fish as a means of control is generally unsuccessful because removal of large adults from the population leads to a

decrease in density dependence, which decreases natural mortality and increases juvenile recruitment (Rose et al. 2001). For example, a study examining the compensatory responses of a carp population to commercial harvest in a Midwestern lake, determined that survival rates only decreased by 25% at a 43% exploitation rate (Weber et al. 2016). This demonstrates that established populations of mature carp can regulate recruitment and survival rates, and that removal methods that reduce the adult population can initiate compensatory responses (Healey 1980). Furthermore, the large number of juvenile carp recruited after removals targeting adults may lead to a rapid increase in carp biomass if future removal goals are not achieved (i.e. missed harvest targets, low budgets, inclement weather; Colvin et al. 2012b).

Managers have been looking for alternative methods targeted outside of the adult life stage to reduce the overall carp biomass, and it is thought that the targeting of the larval life stage via electroshocking may be an underutilized form of control (Natile et al. 2013; Gross et al. 2015; Simpson et al. 2016, 2018). Prior to this modeling project there had not been an explicit effort to evaluate embryo electroshocking as a removal mechanism to control invasive carp populations. A study conducted in a laboratory setting on Rainbow Trout (*Oncorhynchus mykiss*) concluded that electricity could be used to increase embryo mortality if applied prior to the eyed embryonic stage (Gross et al. 2015; Simpson et al. 2016). Our model simulations suggest that active control of carp via embryo electroshocking alone will have little effect on the overall carp biomass. These results are due to the large mortality rates naturally imposed at the larval stage, thus the added mortality rate via embryo electroshocking leads to an alleviation of density dependent mortality on the remaining larval and juvenile carp. For instance, when an embryo electroshocking rate of 0.5 (i.e. 50% mortality) is imposed for 30 years, the annual recruitment at the end of the simulation only drops by $\approx 20\%$. This is due to a compensatory response in which recruitment and survival increase in response to a perturbation in the population. A similar response was found for juvenile trapping, which alone, was unsuccessful at significantly reducing overall carp biomass. This is again due to density dependent feedbacks, whereby removing juveniles reduces density dependent mortality on the remaining population (Rose et al. 2001).

Our findings suggest that intensive carp removal efforts that target multiple life-stages may be necessary to overcome compensatory feedbacks. When two or more removal efforts were conducted in tandem, there was a higher likelihood—at a given removal rate—of reducing carp biomass below the ecological recovery threshold. These findings demonstrate the importance of targeting multiple life stages to significantly reduce the biomass of nonnative species. For instance, a modeling project that investigated mechanical removals of nonnative Lake Trout (*Salvelinus namaycush*) in Swan Lake, Montana determined that the harvest of adults could potentially lead to an increase in the overall population, but harvest of both the adult and juvenile life stages could lead to a population collapse (Syslo et al. 2013).

Imposing a mortality rate high enough to achieve modeled populations declines, however, could be difficult for managers at Malheur Lake given the lake size ($\approx 14,000$ ha), amount of potential spawning habitat, the potential for inclement weather (wind, rain, snow, etc.), and amount of labor necessary to implement large scale removals. Even with all three removal methods combined, our results suggest that each method would need to impose relatively high mortality rates ($> 30\%$). That said, there have been studies conducted on smaller systems that were able to demonstrate an ability to impose large mortality on invasive carp populations via commercial harvest. For instance, researchers in the Midwest have imposed high levels of commercial harvest (52–94%) by targeting large carp aggregations which take place in both winter (i.e. predator avoidance mechanism) and spring (i.e. pre-spawning behavior) and are recognized as an exploitable vulnerability of carp (Pitcher and Parisch 1986; Penne and Pierce 2008; Bajer et al. 2011). Furthermore, research conducted in a laboratory setting demonstrated that at power densities ($12,700 \mu\text{W}/\text{cm}^3$) and voltage gradients ($10 \text{ V}/\text{cm}$) the electroshocked carp embryos survival $\leq 50\%$ (ambient conductivity $127 \mu\text{S}/\text{cm}$; Simpson et al. 2018). These researchers further demonstrated that once carp embryos reach pigmentation (≈ 69 h) the embryos become resistant to electroshocking (Simpson et al. 2018). While these results are promising, Malheur Lake is a much larger and more complex system; therefore, the levels needed to be implemented to significantly reduce populations may not be achievable.

Prior to this project, avian piscivory had never been explicitly investigated as a biocontrol mechanism in the suppression of invasive carp. Previous studies had demonstrated that the sole targeting of invasive carp via passive biological control methods (i.e. Northern Pike, *Esox lucius*) had not been successful without prior bio-manipulations (Perrow et al. 1997; Mehner et al. 2004; Colvin et al. 2012b; Davies and Britton 2015). One positive aspect of passive biological control methods such as increased avian piscivory is that these methods can be maintained long term (perpetual maintenance) with little financial input. Our model simulations suggest that avian piscivores contribute to juvenile carp mortality in Malheur Lake; however, a doubling and tripling of the avian piscivore populations had relatively little influence on modeled carp biomass (Fig. 7). Similar to the active control measures, the lack of response to an increase in the avian piscivore populations can be attributed to compensatory responses within the carp population. For instance, when the model was executed with an average number of avian piscivores, the median non-mature carp biomass of $31 \text{ kg}/\text{ha}$ was predicted, however when the avian piscivore populations were doubled and tripled the model predicted a non-mature biomass of 33 and $36 \text{ kg}/\text{ha}$, respectively. Therefore, while not explicitly investigated in this modeling effort, the addition of avian piscivores as a passive removal method would likely be most effective in combination with other current measures of control as a means to potentially offset increased recruitment or survival rates of juvenile carp that are expected in response to active control of older age classes.

Simulations were considered successful if the median model output of carp biomass was reduced below $50 \text{ kg}/\text{ha}$, however it has been demonstrated that as the carp biomass is reduced in a lake, multiple ecological benefits could be realized. For instance, a meta-analysis of laboratory, field, and natural experiments demonstrated that as carp suppression is initiated, improvements have been observed in water quality (nitrogen: $295 \text{ kg}/\text{ha}$, phosphorus $295 \text{ kg}/\text{ha}$, turbidity $256 \text{ kg}/\text{ha}$), vegetation (phytoplankton $160 \text{ kg}/\text{ha}$ and aquatic macrophytes $204 \text{ kg}/\text{ha}$), invertebrates (zooplankton $114 \text{ kg}/\text{ha}$), and vertebrates (fish $100 \text{ kg}/\text{ha}$ and waterfowl $50 \text{ kg}/\text{ha}$; Vilizzi et al. 2015). Thus, even relatively small—and potentially more achievable—reductions in carp populations could have ecological benefits that outweigh the costs

of control efforts, depending on ecosystem recovery targets.

One aspect of CarpMOD that could potentially affect our removal predictions is the omission of immigration and emigration. We chose not to add these fluxes to the population model due to the limited data available on the movement behavior of carp in Malheur Lake. Although conducting model simulations to explore eradication would need to account for these fluxes, it seems unlikely that population movements from tributaries, relative to the number of carp in the lake itself, would significantly influence our general findings (Colvin et al. 2012b). Another aspect of CarpMOD that could potentially affect model predictions is the large uncertainties surrounding model parameters (identified in the sensitivity analysis). While model outputs clearly demonstrate how this uncertainty may affect model results, we also acknowledge that the variability in model outputs could be reduced if an extensive data collection effort was undertaken in Malheur Lake. This data collection effort could help decrease the uncertainty surrounding model parameters, thus decreasing variability in model results and increasing the probability of successful utilization of the model in the future.

Conclusions

Previous modeling efforts have investigated multiple carp control methods (carp separation cages, pheromone-lure traps, commercial harvest, water-level manipulation, cyprinid herpesvirus-3, and sex ratio manipulation), and these studies suggest that carp control would ultimately be unsuccessful without repeated and intensive intervention (Brown and Walker 2004; Weber et al. 2011; Colvin et al. 2012b; Brown and Gilligan 2014; Lechelt and Bajer 2016; Boutier et al. 2019). This study examined three additional novel methods of carp removal (embryo electroshocking, juvenile trapping, and increasing avian predation) both individually and in combination with commercial harvest efforts in order to target multiple life stages. Like previous modeling projects, CarpMOD simulations demonstrated that these innovative removal methods were also unsuccessful without a substantial input of effort. Thus, reducing carp populations in Malheur Lake may require new and innovative control measures. For example, habitat

manipulations, such as lake subdivision or draining may increase the efficiency of control efforts (Griffiths 1978). Such efforts entail very large pulses of investment and infrastructure, however, and more detailed feasibility assessments are likely warranted. Future carp control efforts may also be influenced by changing climate. In the State of Oregon, climate projections (OCCRI 2010), predict that there will be a decrease in summer precipitation and a reduction in winter snowpack in the next 65 years, which will likely lead to a decrease in summer water availability in Malheur Lake (Mote et al. 2018). Although climate projections are inherently uncertain, a next-step could be to use CarpMOD to anticipate opportunities for controlling carp populations under future hydrologic conditions. For instance removal actions targeting carp during low water years when the carp population is concentrated has been suggested (e.g., Ivey et al. 1998), however this may lead to counterintuitive responses due to density-dependent interactions, therefore this uncertainty is further reasoning that models such as CarpMOD should be utilized prior to the implementation of large-scale removal actions.

Our overall findings correspond to the large body of research that illustrates that invasive species can be extremely difficult to control, and in many cases, impossible to eliminate (Epanchin-Niell et al. 2010; Hussner et al. 2017; Rytwinski et al. 2018). This is particularly true for species such as Common carp, which exhibit strong density-dependent responses to control measures (Thresher 1996; Weber and Brown 2013, 2016). In these instances, our findings support those of other studies (Weber and Brown 2009; Lechelt and Bajer 2016), which illustrate that control measures across multiple life-stages may be needed to significantly reduce populations over long time scales. In practice, however, this may require a long term and sustained commitment to removal that may be ecologically or socially untenable in many circumstances (Güneralp and Barlas 2003; Epanchin-Niell et al. 2010). In all these cases we strongly encourage the development of simulation models, such as the CarpMOD developed here, which provide a structured approach for informing invasive species management efforts to effectively condition stakeholder expectations prior to implementing expensive and uncertain control measures.

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Appendix 1: CarpMOD—population dynamics model equations and parameters

State variable equations

Carp population dynamics at time (t) can be described as:

$$[\text{Age } 1 \text{ Abundance}]_t = [\text{Age } 1 \text{ Abundance}]_{t-1} + [\text{Recruitment}]_t - [\text{Age } 1 \text{ Mortality}]_t - [\text{Age } 1 \text{ Survival}]_t$$

$$[\text{Age } x \text{ Abundance}]_t = [\text{Age } x \text{ Abundance}]_{t-1} + [\text{Age } x-1 \text{ Survival}]_t - [\text{Age } x \text{ Mortality}]_t - [\text{Age } x \text{ Survival}]_t$$

$$X = \text{Age } 2, 3, 4, \dots, 20.$$

However, because CarpMOD is ran on an annual timestep, the above equations can be simplified to:

$$[\text{Age } 1 \text{ Survival}] = [\text{Recruitment}] - [\text{Age } 1 \text{ Mortality}].$$

$$[\text{Age } X \text{ Survival}] = [\text{Age } X-1 \text{ Survival}] - [\text{Age } X-1 \text{ Mortality}].$$

$$X = \text{Age } 2, 3, 4, \dots, 20.$$

Von Bertalanffy growth model

The Von Bertalanffy's Growth Model (VBGM) was used to describe the average yearly growth in length of individual carp in the population (Von Bertalanffy 1938). The VBGM equation is:

$$L_{(A)} = L_{\infty} \left(1 - e^{-k(A-t_0)} \right)$$

where $L_{(A)}$ is the length (mm) of the carp at age, L_{∞} is theoretical maximum length, k is the growth coefficient, and t_0 is the theoretical length of the carp at age zero (Von Bertalanffy 1938; Quist et al. 2012). The Malheur National Wildlife Refuge (MNWR) staff collected 88 carp of varying sizes (190–740 mm), over a two year time frame (June 2010–July 2011), using multiple gear types (i.e. electrofishing, dip netting, minnow trapping, angling, trammel netting, and cast

netting). The MNWR staff recorded the total length (mm) of each individual carp and then removed the otoliths using standard removal methods (Secor et al. 1991). Otoliths were processed at Iowa State University and ages were estimated for each individual carp collected (Colvin et al. 2012a). The VBGM was fit using the length and age data in the fisheries stock assessment package (FSA), using the R statistical computing software (mean $\pm$ Standard Error (SE); $L_{\infty} = 818.02754 \pm 41.3931$, $k = 0.13327 \pm 0.01938$, and $t_0 = -0.5482 \pm 0.25022$; R Development Core Team 2017; Ogle 2017, Ogle et al. 2017).

Length–weight relationship

A length to weight relationship was created using data collect during a five day commercial fishing effort (2014) in Malheur Lake, in which 6797 carp were caught and a subsample of 880 carp (85–853 mm) were sampled for their length (mm) and weights (g). This data was analyzed via a logarithmic weight to length relationship created in the FSA package using the R statistical computing software (Bister et al. 2000; Carlander 1969; Ogle 2017). The length–weight relationship equation is,

$$W = aL^b$$

where W is the weight (g), L is the length (mm), a and b are constants that are estimated by linear relationship described above (mean $\pm$ SE; $a = 4.531975 \pm 0.03952$ and $b = 2.869073 \pm 0.01461$; Schneider et al. 2000; Ogle 2017).

Probability of maturity

Carp mature at different rates, therefore an equation that uses length to determine probability of maturity at each age in the carp population was necessary in this model. The probability of maturity equation is,

$$\rho_i = \left(1 + e^{\ln((19)(L_{(A)}) - LM50)/(LM50 - LM95)} \right)^{-1}$$

where ρ_i is the probability of maturity, $L_{(A)}$ is the length at age, LM50 is the length (mm) at 50% maturity, and LM95 is the length at 95% maturity (Brown et al. 2003). The values for the parameters used in this model were derived from the means and standard deviations of the LM50 and LM95 of the

female populations used in CarpSIM (mean $\pm$ standard deviation (SD); LM50 = 309.667 ± 31.754 and LM95 = 364.667 ± 47.343 mm; Brown and Walker 2004; Brown and Gilligan 2014).

Ricker recruitment equation

Recruitment is thought to be density dependent due to the yearly suppressing of age 0 carp via spawning habitat degradation or competition for resources with large adult carp (Rose et al. 2001; Weber et al. 2016). The Ricker Recruitment equation has been demonstrated to be suitable for carp population models (Bajer et al. 2015; Weber and Brown 2013). The recruitment equation is,

$$R = a * S * \exp(-\beta * S)$$

where R is the total annual individual recruits per hectare, S is the numbers of mature individuals per hectare, α is the coefficient that is density-independent, and β is the coefficient that is density-dependent (Ricker 1954). The Ricker Recruitment is recalculated at each progressive time step in order to increase and decrease the recruits into the model as the carp population fluctuates over time. The Ricker Recruitment equation parameters that were used in this model were established by deriving the means and standard deviations of α and β coefficients used to model the carp populations in CarpSIM (mean $\pm$ SD; $\alpha = 20.0825 \pm 16.1242$ and $\beta = 0.0162 \pm 0.0039$; Brown and Walker 2004; Brown and Gilligan 2014).

Annual natural mortality

The annual mortality rate is thought to be density dependent; therefore, an annual mortality rate that fluctuates with the density of carp was necessary in this model. The annual natural mortality rate equation is,

$$V_{(A)} = 1 - e^{-0.006 \left(-\frac{L_{(A)}}{L_{\infty}} \right) - 1.5} + 10^{-4} \cdot D$$

where V is the annual mortality, A is the age of carp, D is the density of age 1 + carp (kg/ha), $L_{(A)}$ is the average length (mm) of carp at age, and L_{∞} is theoretical maximum length of carp in the population (Charnov et al. 2013; Bajer et al. 2015). The annual

mortality rate is recalculated at each progressive time step in order to increase and decrease the mortality as the carp density fluctuates over time.

Appendix 2: Modeled avian piscivory

Avian predation was added to the carp population model in order to more accurately depict the annual mortality imposed on carp by native avian piscivores (Double-crested Cormorant (*Phalacrocorax auritus*), American White Pelican (*Pelecanus erythrorhynchos*), and Caspian Tern (*Hydroprogne caspia*). The addition of avian predation into the model brings more realism to the carp population model as well as enables managers to simulate removal strategies that include increasing the avian populations (e.g., by enhancing nesting habitat). In order to add avian predation into the model we used a bioenergetics approach to estimate the annual consumption of the three avian species (Wiens and Scott 1975; Roby et al. 2003).

In order to quantify the total carp consumed annually, we estimated the annual intake of carp needed to sustain the avian predator populations using a variety of input data. Some required data were available as a product of unrelated studies (Bird Research Northwest 2013, 2014, 2015); where data were not available from Malheur Lake, values were derived from the literature (Table 3).

Rearing chicks were not taken into account in this model because the overall bird productivity at Malheur Lake is poor compared to other nesting locations.

Caspian Tern diet composition was estimated using visual identification of prey species carried back to the colony (for mates or offspring) in the Caspian Tern bill by observers using binoculars from blinds adjacent to the breeding colony (Bird Research Northwest 2013, 2014, 2015). Prior research has demonstrated that the prey species transported back to the colony by Caspian Terns consists of the same general taxonomic composition as their individual diet (Collis et al. 2002). The length of each prey was estimated by comparing the length of fish to that of the Caspian Tern's bill (~ 8 cm; Antolos et al. 2005; Bird Research Northwest 2013, 2014, 2015). We translated the lengths of carp consumed into biomass of carp consumed using a previously documented weight-length relationship (Schneider et al. 2000), which

Table 3 Parameters used as inputs into the avian bioenergetics for the three avian piscivores (Double-crested Cormorant, American White Pelican, and Caspian Tern)

Parameters	Tern	Cormorant	Pelican	References
Average body mass (g)	650	2275	7000	Evans and Knopf (1993), Lyons (2010)
Field metabolic rate (kJ/day)	11.49 m ^{0.718}	11.49 m ^{0.718}	3.90 m ^{0.87}	Ellis and Gabrielsen (1984)
Assimilation efficiencies	0.75	0.75	0.75	Brugger (1993); Miller and Reinecke (1984), Lyons and Roby (2011)
Average abundance	522	247	2719	Bird Research Northwest (2013–2015)
Average days present	100	100	100	Bird Research Northwest (2013–2015)
Energy densities of carp (kJ/g)	6.98	6.98	6.98	Schreckenbach et al. (2001)

The m in the field metabolic rate denotes the mass (g) of individual birds

allowed Caspian Tern consumption of carp to be broken down by carp age class.

Diet data for cormorants and pelicans were lacking for Malheur Lake. The diet composition established for terns was used for cormorants because the two species have displayed generally similar diets in other locations (Collis et al. 2002; Lyons 2010), particularly in shallow water environments. The diet composition of pelicans was assumed to be 50% carp, consistent with limited empirical evidence from a somewhat similar Great Basin large water body (Pyramid Lake, Nevada) that had also been previously invaded by nonnative carp (Hall 1925). The age distribution of carp consumed by pelicans was assumed to be split between two age groupings: 90% juveniles (age 0–3) and 10% adults (age 4+). We calculated the relative diet composition of pelicans contributed by each specific age class using the following equation, which assumed consumption was proportional to the relative availability of each age class:

$$Pr_x = D_y \left(\frac{B_x}{B_y} \right)$$

where x denotes individual age class (i.e. age 1, 2, 3, ...) and y denotes the age grouping (juveniles or adults), B_x is the biomass of each individual age class, B_y is the biomass of each age grouping (juveniles or adults), D_y is the diet composition for each age grouping, and Pr_x is the resulting proportional diet composition of each age class. The sensitivity of model output to this distributional breakdown was tested by running multiple scenarios assuming different age class (length) distributions of carp consumed. We determined that shifts in the age/size of the

pelican's prey had little to no effect on the output of carp biomass over time; therefore, we only considered the above distribution in subsequent analyses.

Avian piscivore diets were allowed to shift in response to fluctuations in carp densities that will occur as simulated removal actions are implemented following a predator–prey functional response. Diet shifts associated with changes in prey densities have been seen previously in piscivorous waterbird populations. For instance, Double-crested Cormorants shifted their diets away from largely limnetic fish species [Alewife (*Alosa pseudoharengus*), Yellow perch (*Perca flavescens*), and three spine stickleback (*Gasterosteus aculeatus*)] to a benthic fish species [Round goby (*Apollonia melanostoma*)] during the Goby's proliferation and subsequent invasion of the Great Lakes (Johnson et al. 2015). We investigated multiple functional response relationships (constant, type 1 [linear], type 2 [saturation], type 3 [sigmoid]) between diet and juvenile carp densities. We determined that the type 1 functional response (% of diet that was carp = 0.0041 multiplied by the juvenile carp biomass) adequately described the likely diet shifts that would take place as carp densities varied as removal efforts were implemented and parsimoniously minimized the number of additional assumptions needed (i.e. rate of saturation or sigmoid shape).

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