

ARTICLE

Freshwater Ecology

Controlling invasive fish in fluctuating environments: Model analysis of common carp (*Cyprinus carpio*) in a shallow lake

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Handling Editor: Matthew Troia**Abstract**

Climate change can act to facilitate or inhibit invasions of non-native species. Here, we address the influence of climate change on control of non-native common carp (hereafter, carp), a species recognized as one of the “world’s worst” invaders across the globe. Control of this species is exceedingly difficult, as it exhibits rapid population growth and compensatory density dependence. In many locations where carp have invaded, however, climate change is altering hydrologic regimes and may influence population demography and efficacy of human control efforts. To further evaluate these processes, we employed a modified version of an age-based population model (CarpMOD), to investigate how hydrologic variability (change in lake area) influences carp population dynamics and control efforts in Malheur Lake, southeastern Oregon, USA. We explored how changes in lake area influence carp populations under three control scenarios: (1) no carp removal, (2) carp removal during low water years, and (3) carp removal during all years. Lake area fluctuations strongly influenced carp populations and the efficacy of carp control. Modeled carp biomass peaked when the lake transitioned from high-to-low levels, and carp biomass declined when lake area transitioned from low-to-high. Removing carp during low water periods—when fish were concentrated into a smaller area—reduced carp populations almost as much as removing carp every year. Furthermore, the effectiveness of control efforts increased with the prevalence and severity of low lake conditions (longer durations of very low lake area). These simulations suggest that a drier climate may naturally decrease carp populations and make them easier to control. However, drier conditions may also negatively affect aquatic ecosystems and potentially have a greater impact than non-native species themselves.

KEYWORDS

CarpMOD, climate change, common carp, ecological modeling, hydrologic variability, pest control, shallow lake, wetland management

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INTRODUCTION

Humans have altered freshwater ecosystems directly via water pollution, flow modification, degradation of habitat, fisheries overexploitation, introductions of non-native species, and indirectly via anthropogenic climate change (Ashizawa & Cole, 1994; Poff & Hart, 2002; Strayer & Dudgeon, 2010). Individually, these alterations have had negative impacts on native species and overall biodiversity (Dudgeon, 2010; Dudgeon et al., 2006), but cumulative effects resulting from interactions among these factors are also important. An example is the interaction between climate change and the spread of non-native species, which collectively pose urgent threats to global freshwater biodiversity (Hellmann et al., 2008; Perrings et al., 2000; Roy et al., 2014). By altering the physical and hydro-chemical conditions of freshwater ecosystems, climate change can influence the spread and establishment of non-native species, as well as efforts to control and suppress these invaders (Dunham et al., 2020; Rehage & Blanchard, 2016). The effectiveness of non-native species control strategies is of specific importance because these efforts are crucial to mitigating the impacts of non-native species on freshwater ecosystems (Hellmann et al., 2008).

Common carp (*Cyprinus carpio*) is recognized as the eighth most prevalent non-native species in the world (Lowe et al., 2000) and can attain extremely high population abundance due to their high capacity for population growth and expansion (Britton et al., 2010; Gehrke & Harris, 2000; Pietsch & Hirsch, 2015). Once common carp (hereafter “carp”) are found in a novel habitat, managers frequently implement control measures to halt further spread and control population size (Lodge et al., 2006; Sakai et al., 2001). Control that targets the adult life stage has been demonstrated to be an efficient and cost-effective removal method in some contexts (Colvin et al., 2012; Pearson et al., 2019). However, efforts to control carp populations have also resulted in unexpected outcomes, such as removal efforts that result in greater population densities (Pine III et al., 2009). These seemingly counterintuitive responses are a consequence of positive feedback and negative feedback that control carp population dynamics. Carp exhibit strong density dependence in which demographic rates (i.e., mortality and recruitment) shift in response to variations in the population’s overall density (Healey, 1980; Rose et al., 2001; Weber et al., 2016). For instance, removing adult carp from a population can alleviate density dependence, resulting in higher juvenile recruitment (Colvin et al., 2012; Healey, 1980; Weber et al., 2016).

In the last decade, several models have been developed explicitly to help understand and anticipate the population dynamics of carp (e.g., Brown & Gilligan, 2014;

Colvin et al., 2012; Pearson et al., 2019). However, as is often the case for population dynamics models, these models generally assume that the environment—such as the availability of habitat—is unchanging or stationary. This simplification enables model users to isolate the effects of carp control without the added complexity of a variable natural environment (Brown & Gilligan, 2014; Colvin et al., 2012; Pearson et al., 2019). A limitation of this approach, however, is that environmental fluctuations may dampen or facilitate the effects of control measures on population dynamics. For instance, lower water levels may concentrate carp populations in a smaller area, potentially boosting the effects of removal efforts relative to times when water levels are higher (Maiztegui et al., 2019).

Understanding the effects of environmental fluctuations on the ability to control non-native species is critical because such dynamics are being altered by a changing climate (Reidmiller et al., 2018). In many of the freshwater ecosystems where carp have invaded, climate change influences the frequency and magnitude of high and low water levels (Adrian et al., 2009). For instance, in the Great Basin region of the United States—where many freshwater habitats have been invaded by carp—climate change projections predict a decrease in the annual snow water equivalent and more frequent droughts (low spring snowpack; Dalton et al., 2018; Lute et al., 2015; Mote et al., 2018; Snyder et al., 2019), which, in turn, are likely to reduce the size of lakes, rivers, and wetlands that carp occupy.

In this study, we employed a system dynamic modeling approach (Ford, 1999; Meadows, 2008) to evaluate how fluctuations in water availability may influence the population dynamics of carp and the efficacy of carp control efforts. We addressed two questions: (1) How do natural fluctuations in lake area influence carp population dynamics and control efforts? and (2) How might alterations to lake area with climate change influence carp abundance and control efforts? To address these questions, we employed a modified version of an age-based population model (CarpMOD; Pearson et al., 2019). Our case study system was Malheur Lake, a large wetland lake system in the Great Basin region of southeastern Oregon with an established carp population. We parameterized the model with 80 years of reconstructed lake areas to explore how current and historical lake area fluctuations influence carp population and control efforts. We conducted a series of simulations to explore how changes to lake area—expected to occur with changing climate—may alter carp population dynamics and the ability of humans to intervene to effectively control populations. One of our primary objectives was to target potential vulnerabilities within carp populations brought on by natural hydrologic cycles and potential future

climatic variation: information that can be used by managers when attempting to control carp in locations that have highly variable hydrologic environments.

METHODS

Study area

The system we modeled is Malheur Lake (elevation = 1248.75 m), a large (average $\approx 19,600$ ha), shallow (average depth ≈ 0.58 m; max depth ≈ 1.26 m), and terminal lake (endorheic basin) located within the Malheur National Wildlife Refuge (MNWR) in the Great Basin of southeastern Oregon (lat 43.3115° , long -118.7952°). Malheur Lake experiences large fluctuations in size, which in

recent times have ranged from approximately 550 ha in 1992 to 51,500 ha in 1986 (Figure 1). Fluctuations in lake area are primarily driven by precipitation runoff and evapotranspiration (Hamilton et al., 1986; Hubbard, 1975). Precipitation falls primarily as snow and accumulates in the Steens and Blue Mountains, melting in the spring and early summer. Runoff enters the lake via the Silvies and Donner und Blitzen (hereafter “Blitzen”) Rivers, which drain a total area of ≈ 7770 km² (Adjei et al., 2015; Miller, 2012).

Modeling the area of Malheur Lake

To examine how natural fluctuations in Malheur Lake influence carp population dynamics, we reconstructed

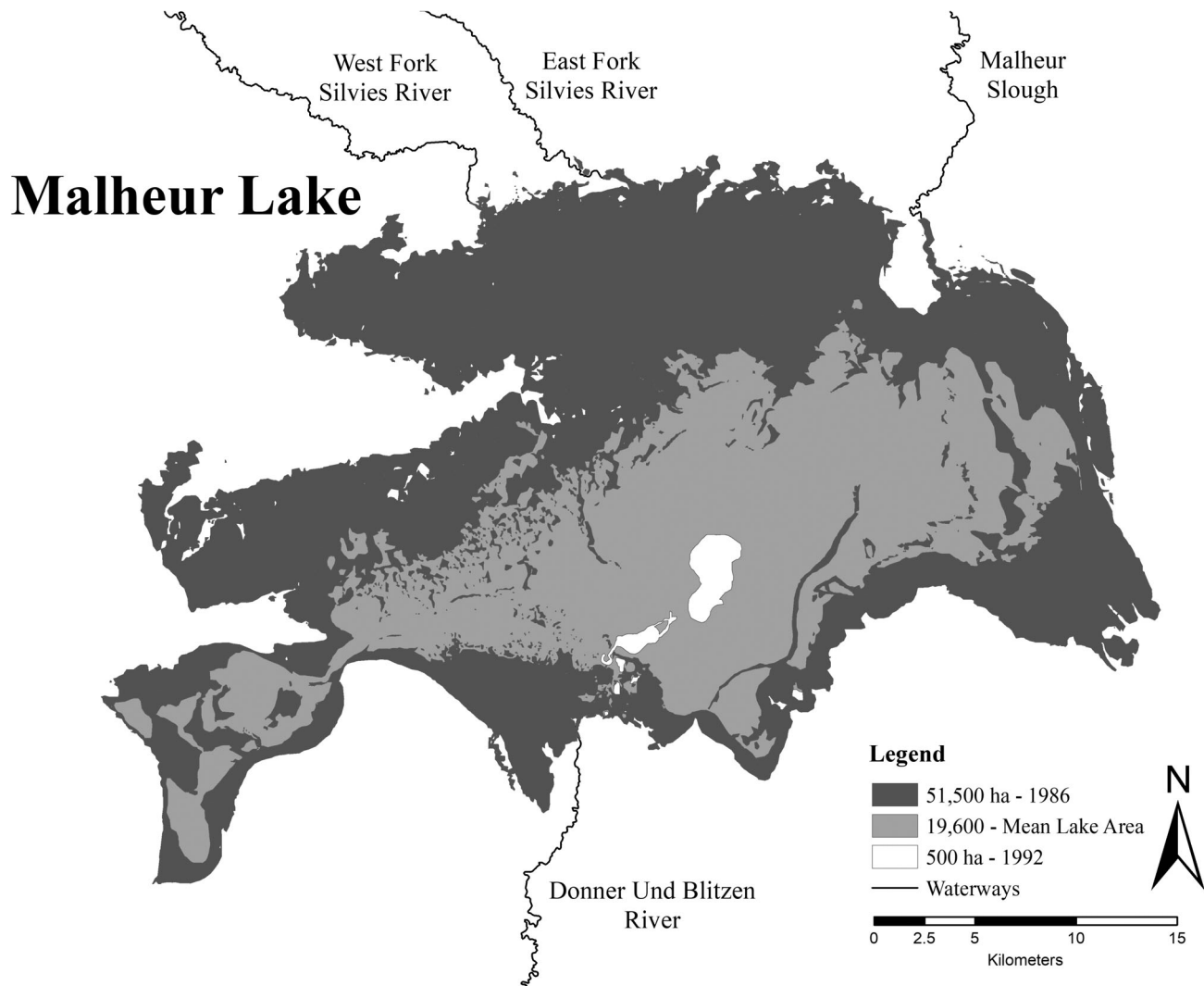


FIGURE 1 Map of Malheur Lake located within the Malheur National Wildlife Refuge in southeastern Oregon. The dark gray region depicts the maximum lake area extent in 1986 ($\approx 51,500$ ha), the gray region depicts the average fall lake area ($\approx 19,600$ ha), and the light gray region depicts the lowest lake area extent in 1992 (≈ 550 ha)

lake areas for an 80-year period from 1938 to 2018. Periodic observations of lake area have been collected at Malheur Lake by the MNWR refuge staff since 1938; however, much of these data are qualitative and there are large gaps in observations (Duebbert, 1969). We reconstructed lake area by building a basic hydrologic model that predicts autumn lake area (1 October) using a collection of satellite images and environmental variables (1978–2018; Appendix S1). Lake areas were quantified for 1 October because this represents the time of year when lake area is generally lowest, and thus, it is likely the time of greatest density-dependent interactions within the carp population (i.e., increased natural mortality).

The most parsimonious model predicted lake areas that closely matched observed lake area dynamics of Malheur Lake during the years in which empirical lake area estimates were available ($R^2 = 0.948$; adjusted $R^2 = 0.943$; $F_{3,32} = 193.9$; $p < 2.2e^{-16}$; Figure 2). Lake area was best predicted by: (1) previous year's lake area (in hectares), (2) discharge (centimeters; water year: 1 October–30 September) from the Donner und Blitzen

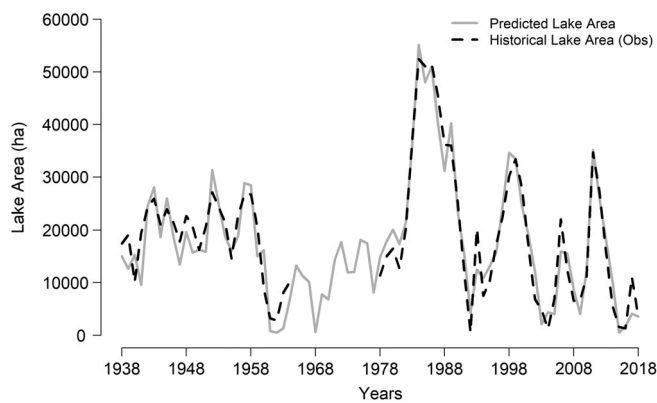


FIGURE 2 Reconstructed historical lake areas (1938–2018) based on a predictive multiple regression model. The solid gray line indicates modeled lake area, and the black dashed line indicates historical observations of lake areas

River, and (3) date of 50% of total discharge (Julian date) from the Donner und Blitzen River (Appendix S1).

Model description: CarpMOD

To simulate carp population dynamics, we used CarpMOD (Pearson et al., 2019), which was originally constructed in STELLA 10.0.6 (ISEE Systems, Inc., Lebanon, NH, USA) as a non-sex-specific, deterministic model, executed on an annual time-step. CarpMOD uses governing equations to simulate carp abundance, age structure, and size (length and weight; Table 1). Juvenile carp recruit into the population based on the Ricker recruitment model after completing their first year of life (age 1), where recruitment is a density-dependent relationship between spawning adults and the number of age-0 juvenile recruits (Brown & Walker, 2004; Koehn et al., 2000; Ricker, 1954). The Ricker recruitment model consists of R , which is the total annual recruits per hectare (total recruits equal the recruits per hectare multiplied by lake area); S , which is the number of mature individuals per hectare (a number of mature carp per hectare equal the total mature carp population divided by lake area); α , which is the density-independent coefficient; and β , which is the density-dependent coefficient (Table 1, Equation (1); Ricker, 1954).

Juvenile carp that recruit into the model are tracked by age, from age 1 to age 20. Annual mortality is a density-dependent function based on the carp length at age and the biomass density of the carp population (age 1+; in kilograms per hectare), whereby smaller carp experience greater mortality (Bajer et al., 2015; Charnov et al., 2013). The annual natural mortality equations consist of $V_{(A)}$, which is the annual mortality of carp at age A ; $L_{(A)}$, which is the average length of carp at age A ; L_{∞} , which is the asymptotic average length of the carp population; D , which is the density of age 1+ carp (in kilograms per

TABLE 1 Equations used in CarpMOD1.5 to simulate the population dynamics of carp in Malheur Lake (Pearson et al., 2019)

Equation no.	Model component	Equation
1	Ricker recruitment model	$R = \alpha \times S \times \exp(-\beta \times S)$
2	Annual natural mortality (<250 mm)	$V_{(A)} = 1 - e^{-0.06 \left(\frac{L_{(A)}}{L_{\infty}} \right)^{-1.5}} + 10^{-4} \cdot D$
3	Annual natural mortality (>250 mm)	$V_{(A)} = \left(1 - e^{-0.06 \left(\frac{L_{(A)}}{L_{\infty}} \right)^{-1.5}} + 10^{-4} \cdot D \right) \times (1 - AR)$
4	von Bertalanffy growth model	$L_{(A)} = L_{\infty} (1 - e^{-k(A-t_0)})$
5	Length to weight	$W = aL^b$
6	Probability of maturity	$\rho_i = \left(1 + e^{(\ln(19) \left((L_{(A)} - LM_{50}) / (LM_{50} - LM_{95}) \right))} \right)^{-1}$
7	Adult reduction rate	$AR_T = \left(\frac{LA_F}{LA_A} \right) F_{eff}$

hectare; density of age 1+ carp equals the total age 1+ carp divided by lake area), and AR, which is the adult reduction rate (AR) (Table 1, Equations (2) and (3); Bajer et al., 2015; Charnov et al., 2013; Pearson et al., 2019).

Carp that survive increase in length each year based on a von Bertalanffy growth model (VBGM) and in weight based on an empirical length–weight relationship (Jackson et al., 2008; Schneider et al., 2000; von Bertalanffy, 1938). The VBGM equation consists of $L_{(A)}$, which is the length (in millimeters) of carp at age A (in years); L_{∞} , which is the theoretical maximum length; k , which is the growth coefficient; and t_0 , which is the theoretical length of carp at age zero (Table 1, Equation (4); von Bertalanffy, 1938). The length-to-weight equation consists of W , which is the weight (in grams); a and b , which are constants estimated via regression analysis; and L , which is the length (Table 1, Equation (5); Schneider et al., 2000).

The proportion of mature carp at each age class is determined via a probability of maturity equation (Brown et al., 2003; Brown & Walker, 2004). The probability of maturity equation consists of ρ_i , which is the probability of maturity; $L_{(A)}$, which is the length at age A ; LM_{50} , which is the length at 50% maturity; and LM_{95} , which is the length at 95% maturity (Table 1, Equation (6); Brown et al., 2003).

Due to the prevalence of avian predation in Malheur Lake by double-crested cormorant (*Phalacrocorax auritus*), American white pelican (*Pelecanus erythrorhynchos*), and Caspian tern (*Hydroprogne caspia*), avian mortality functions were included in the model to account for the annual consumption of small carp (<age 4) by these avian piscivores (Pearson et al., 2019; Roby et al., 2003; Wiens & Scott, 1975). The avian piscivore diets shifted in response to fluctuations in carp densities that occurred during simulations brought on by carp removal actions or natural population dynamics, and the shifts in diet followed a type 1 predator–prey functional response (Pearson et al., 2019). A more in-depth breakdown of the avian mortality functions used to determine annual avian predation can be found in Pearson et al. (2019).

The model calculates the biomass density of carp per hectare of lake area (in kilograms per hectare) and assumes that the carp are uniformly distributed throughout the lake (Appendix S2). Therefore, in years in which the lake area increases, the total carp population is initially the same, but the biomass density (in kilograms per hectare) decreases due to the same number of carp evenly spread over a greater area.

We simulated the carp population response to harvest of adult carp (>250 mm $\approx$ age 3+), which is widely viewed as a preferred method due to the low cost of implementation and reduced mortality of nontarget species (Colvin et al., 2012). The AR is the proportion of adult carp removed annually and is assumed to be

proportional to the area of the lake (Table 1, Equation (7); Figure 3). This is based on the assumption that while the lake area may increase and decrease annually, the lake area fished (i.e., area of nets set) remains constant (i.e., number of nets owned remains fixed year to year). Therefore, the resulting removal rate will be higher when the lake area is small and lower when the lake area is large. The AR equation consists of LA_F , which is the lake area fished (5000 ha); LA_A , which is the lake area actual (in hectares); and F_{eff} , which is the fishing efficiency (0.95). This relationship assumes that harvest pressure (e.g., the area of the lake that nets are set, 5000 ha) remains the same across different lake areas, which results in lower removal rates when the lake is large.

The population dynamic model parameters described earlier were provided by Pearson et al., 2019, in which means and standard deviations were determined from in situ data as well as multiple literature sources, where local data were unavailable (Table 2). A global sensitivity analysis demonstrated how uncertainty in the value of model parameters affected model outputs, and the researchers determined that the simulated carp biomass (in kilograms per hectare) was most sensitive to uncertainty in parameters controlling density-dependent recruitment (α , recruitment coefficient), length at age relationship (k , growth coefficient), and the length–weight relationship (b , weight length coefficient; Pearson et al., 2019).

Carp model scenarios

We first used CarpMOD (Pearson et al., 2019) to simulate historical carp population fluctuations using the reconstructed lake areas (1938–2018) and tested the effects of three alternative carp management strategies: (1) no removal of carp (No); (2) low water year removal (Low), whereby carp are removed when lake area is below 10,000 ha; and (3) all year removal (All), where carp are removed every year (even when lake levels are

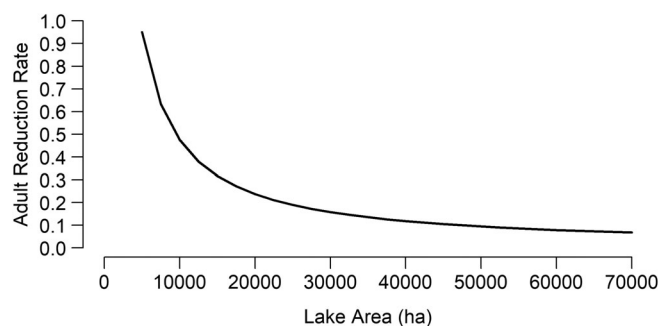


FIGURE 3 Assumed adult carp reduction rate in relation to the area of Malheur Lake used in model simulations

TABLE 2 Parameter values and standard deviations (SD) used in carp population model simulations

Parameters	Symbol (units)	Function	Value	SD
Alpha coefficient ^a	$a (\times 10^{-5})$	W-L	4.531	0.0395
Beta coefficient ^a	b	W-L	2.869	0.015
Theoretical length at age 0 ^a	t_0 (mm)	VBGM	-0.548	0.250
Growth coefficient ^a	K (years ⁻¹)	VBGM	0.133	0.020
Theoretical max length ^a	L_∞ (in millimeters)	VBGM	818.028	41.393
Alpha coefficient ^b	α	Recruitment	20.083	16.124
Beta coefficient ^b	β	Recruitment	0.0162	0.004
Length of maturity 50 ^b	LM_{50} (mm)	Maturity	309.667	31.754
Length of maturity 95 ^b	LM_{95} (in millimeters)	Maturity	364.667	47.343
Lake area fished	LA_F (in hectares)	AR	5000	...
Fishing efficiency	F_{eff}	AR	0.95	...

^aDerived via data collected from Malheur Lake.

^bBrown & Walker, 2004; Brown & Gilligan, 2014.

high). For carp removal scenarios, we assumed that the lake area fished (LA_F) was 5000 ha, which is a value similar to historical carp removal fishing rates in Malheur Lake. We also conducted a sensitivity analysis to examine a range of lake areas fished (2500, 5000, and 7500 ha) identified as feasible by stakeholders at Malheur Lake (i.e., most ambitious, 7500 ha, to least ambitious, 2500 ha). We conducted an additional sensitivity analysis to evaluate how the assumption of a fluctuating AR may affect model results. We again simulated the historical carp population and applied a range of set removal rates (0.0, 0.25, 0.5, and 0.75), thus demonstrating how the carp population would react if removal rates were not proportional to lake area, and thus simulating the potential for carp to use certain habitats in ways in which capture probability would no longer be linked to lake area.

We then conducted a suite of deterministic simulations to provide additional heuristic insights into how changes in the magnitude and duration of high (HLA) and low lake areas (LLA) may affect carp populations and removal efforts (Figure 4). These scenarios were meant to simulate increased prevalence of drought conditions (e.g., frequency and duration) anticipated for the Great Basin (Dalton et al., 2018; Snyder et al., 2019), which are likely to reduce the number of years of larger lake areas, and decrease the size of the lake during years of both HLA and LLA (i.e., lower highs and lower lows). Three HLA and LLA duration scenarios were selected that represent a progression toward fewer years in which the lake is high: (1) 6 years of high lake area (HLA) and 6 years of LLA (6×6); (2) four high and eight low (4×8); and (3) two high and 10 low (2×10), with the 6×6 scenario roughly representing the current (baseline) hydrologic cycle based on observations over the last 40 years in Malheur Lake (1978–2018). For each duration

scenario, we then adjusted the magnitude of the lake area during high and low years: (1) HLA (max: 30,000; min: 12,500); (2) medium lake area (max: 25,000; min: 7500); and (3) LLA (max: 20,000; min: 2500), with the HLA scenario closely corresponding to historical lake areas for Malheur Lake (historical mean = 19,600 ha). This resulted in a total of nine deterministic lake area fluctuation scenarios (Figure 4). For each of these lake area scenarios, we simulated the overall carp biomass density under three removal scenarios: (1) No; (2) Low; and (3) All. We acknowledge that such periodic hydrologic patterns would not occur naturally in Malheur Lake (or most other shallow lakes); however, the objective of these simulations was to provide a mechanistic understanding of how general changes in the duration and magnitude of lake areas will influence carp populations.

In addition to these deterministic lake area scenario simulations, we also simulated future carp biomasses under stochastic variability in lake areas. To predict future lake areas, we randomly selected parameter values for the hydrologic model each year from a normal distribution based on the mean and standard deviation of the identified predictor variables in the lake area model (Appendix S1). We implemented three future lake area scenarios: (1) base (no change), (2) base -12.5%, and (3) base -25%. The base scenario represented a continuation of existing lake area patterns (1938–2018), and the base -12.5% and base -25% scenarios were based on the annual lake area output from the multiple linear regression model and subtracted 12.5% or 25%, respectively (predicted $\approx 30\%$ decrease in snow water equivalent by midcentury in Pacific Northwest; Mote et al., 2018; Naz et al., 2016). While these future lake area scenarios are roughly based off climate change predictions (Mote et al., 2018; Naz et al., 2016), with so much uncertainty in specific climate change models, our future lake

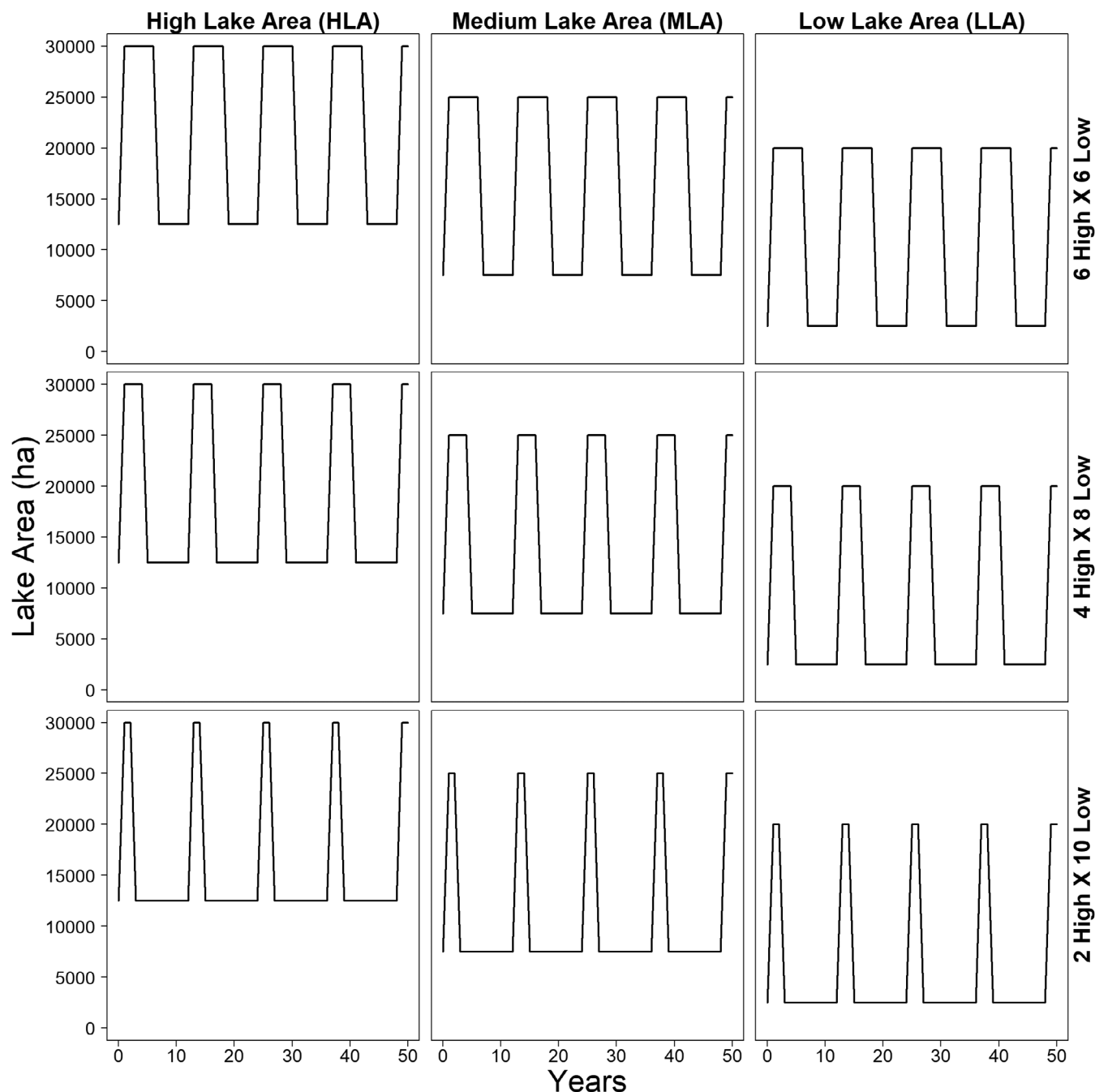


FIGURE 4 Carp population dynamics simulated under nine deterministic lake area scenarios, which represent different combinations of high and low lake areas, including three duration scenarios: (1) six high and six low (6×6 ; top row), (2) four high and eight low (4×8 ; center row), and (3) two high and 10 low (2×10 ; bottom row) and three lake area scenarios: (1) high lake area (HLA—max: 30,000; min: 12,500; left column), (2) medium lake area (MLA—max: 25,000; min: 7,500; middle column), and (3) low lake area (LLA—max: 20,000; min: 2,500; right column). The graph is focused on the first 50 years (out of 80) to demonstrate more detailed lake fluctuations

area scenarios are simply meant to demonstrate how the control of an aquatic invader may shift in the future under a generalized warmer/drier climate.

For each of the scenarios described earlier, two distinct phases were simulated: (1) base simulation phase and (2) scenario implementation phase. The base simulation phase refers to the first 50 years, where lake area is

held constant (median lake area scenario; described in detail below), thus enabling the carp population to reach equilibrium prior to imposing any lake fluctuation or carp removal scenarios. Enabling the population to reach equilibrium prior to the implementation of scenarios enabled us to prevent modeled populations from extinction due to chance fluctuations and ensured that model outputs

reflected the effects that environmental fluctuations and management scenarios had on an established carp population. The implementation phase began at year 51 when the different model scenarios (i.e., lake area fluctuations and carp removals) were imposed and ran for the next 80 years (phase 1 + phase 2 = 130-year model run).

We built demographic stochasticity into the model by specifying the model to randomly choose a value for the α (density-independent) and β (density-dependent) parameters of the Ricker recruitment model from a log-normal distribution each year of the model run (Table 2). We added demographic stochasticity to recruitment because this is a process that is likely to vary year to year due to a variety of factors that are unaccounted for in our model (e.g., water temperature and food availability; Edelman-Keshet, 2005). Furthermore, to explore how uncertainty in other parameters (non-Ricker recruitment parameters; Table 2) may influence model outcomes, we conducted a 10,000-run model uncertainty analysis for each scenario. For each of the 10,000 model runs, random values for each model parameter were selected from a normal distribution with a standard deviation either derived from data collected within Malheur Lake or from the literature. The randomly selected parameter values were then held constant for the duration

of the simulation. Time series graphs were constructed using the median model outputs from the 10,000 model runs, and box-and-whisker plots were constructed to demonstrate the range of modeled outcomes produced with different parameter combinations. For each scenario, we explored how successful removal strategies were at maintaining the carp biomass density below 50 kg/ha, which is the hypothesized threshold at which waterfowl productivity increases, due to increased lake clarity and aquatic vegetation (e.g., aquatic vegetation provides waterfowl food that is critical for reproduction and migration both directly in the form of seed production (carbohydrates) and indirectly by providing habitat for macroinvertebrates (proteins; Hanson & Butler, 1994; Vilizzi et al., 2015).

RESULTS

Carp model scenarios

Model results from the historical carp population simulations suggest that lake area variability strongly controls the carp biomass dynamics in Malheur Lake (Figure 5a). Carp biomass density generally peaked in years following

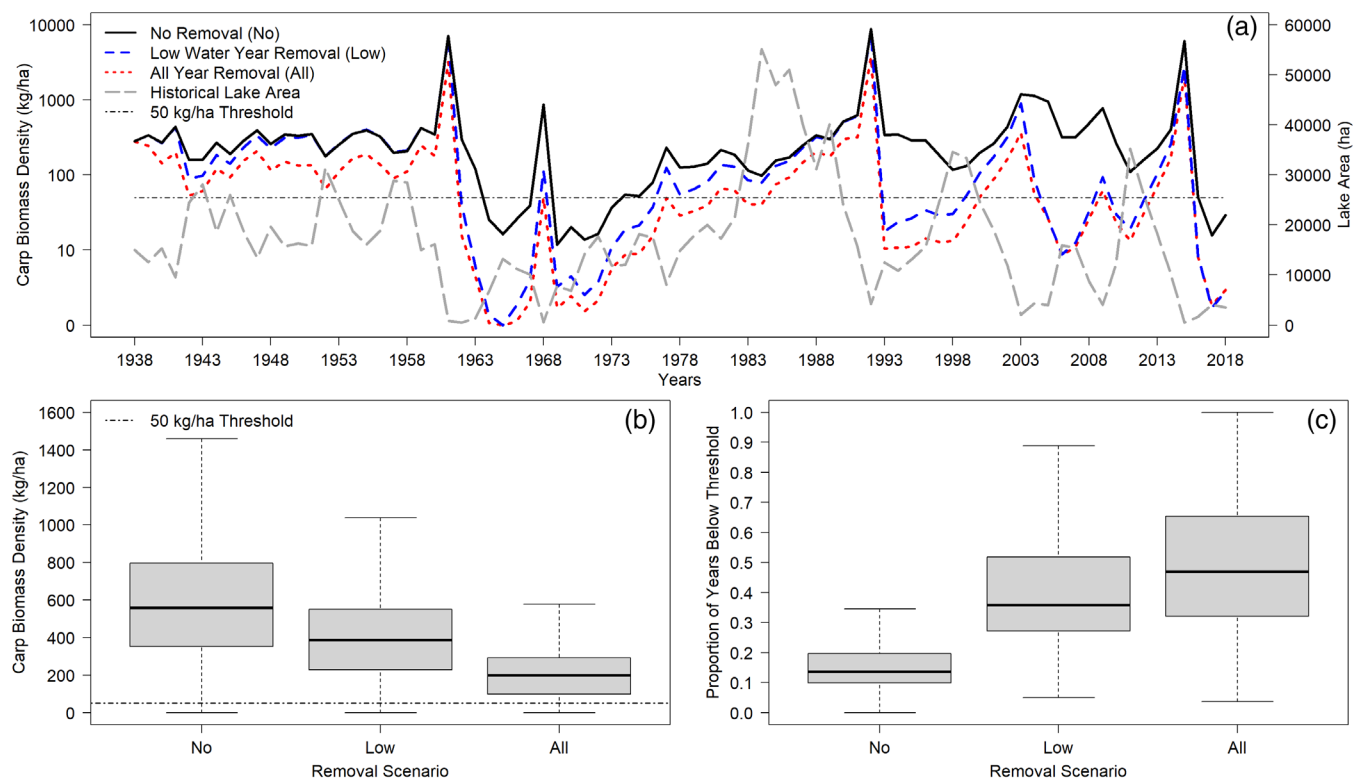


FIGURE 5 Simulated carp biomass density (in kilograms per hectare) under historical lake area conditions (1938–2018) and three carp removal scenarios (a); effects of carp removal on average modeled carp biomass density (in kilograms per hectare) from 1938 to 2018 (b); median proportion of years modeled carp biomass density fell below 50 kg/ha threshold between 1938 and 2018 (c). Box-and-whisker plots (panels b and c) show the sensitivity of modeled outcomes to uncertainty in model parameter values from a 10,000 simulation uncertainty analysis, where the line within each box is the median outcome, box boundaries are 25th and 75th percentiles, and whiskers are 5th and 95th percentiles

large drops in lake area due to the confinement of the population. In contrast, years in which the lake area is increasing, the carp biomass density falls, often dipping below the biomass threshold identified in previous research as necessary to promote aquatic ecosystem recovery (<50 kg/ha; Vilizzi et al., 2015). The historical lake area model with no carp removal (No) produced a carp biomass density of 558 ± 341 kg/ha (median $\pm$ standard deviation; Figure 5b), which fell below the 50 kg/ha threshold in $14 \pm 19\%$ of simulated years (Figure 5c). Outputs from the low water year removal (Low) scenario resulted in a carp biomass density of 388 ± 247 kg/ha with the carp biomass density falling below the designated threshold in $36 \pm 20\%$ of simulated years. Outputs from the all year removal (All) scenarios resulted in a carp biomass density of 200 ± 141 kg/ha, with the carp biomass density falling below the desired biomass threshold in $47 \pm 23\%$ of

simulated years. Modifying our assumptions about lake area fished (2500, 5000, and 7500 ha) only modestly influenced modeled outcomes, with larger areas fished resulting in smaller carp populations (see Appendix S3). However, modifying the proportion of the carp population removed strongly influenced model outcomes (i.e., when we assumed that carp removal rates were independent of changes in lake area). A constant removal rate of 0.25 increased modeled carp biomass densities by 58 kg/ha, while removal rates of 0.5 and 0.75 decreased the median carp biomass densities by 59 and 126 kg/ha, respectively (see Appendix S3).

Deterministic lake area simulations demonstrated that shifts in the magnitude and duration of HLA and LLA can have a large influence on modeled carp biomass. Simulations with a greater duration of high water years (i.e., 6 low $\times$ 6 high years; Figure 4) led to greater mean,

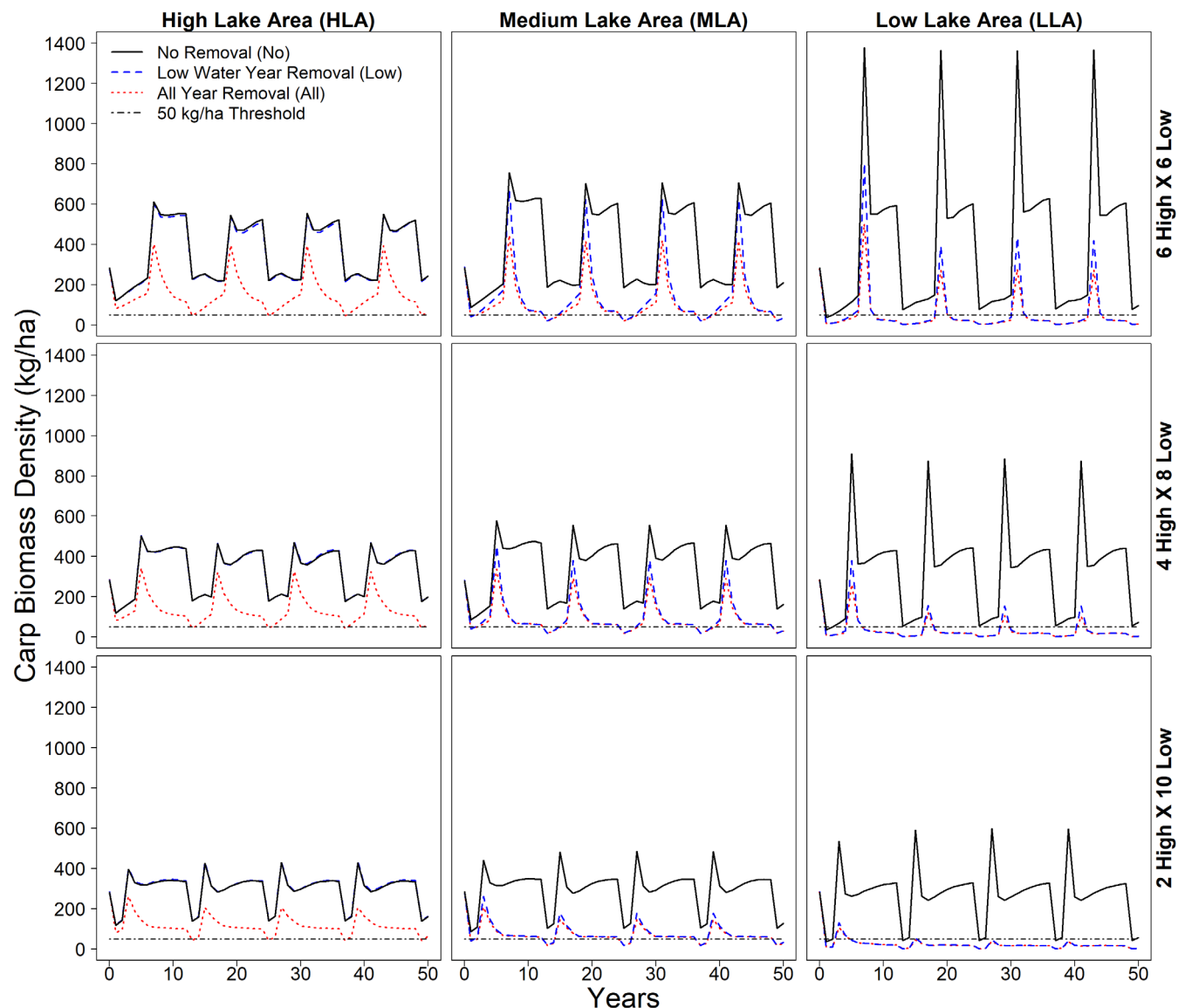


FIGURE 6 Effects of carp removal strategies on modeled carp biomass density (in kilograms per hectare) under different durations of high and low lake area, and different average lake areas (see Figure 4)

maximum, and minimum carp biomass density under all carp removal scenarios (No, Low, and All; Figure 6), whereas decreased duration of high water years (i.e., 2×10) had the opposite result (i.e., lower carp biomasses). The greatest peaks (maximum) in carp biomass density coincided with the LLA scenarios and increased duration of high water years (i.e., 6×6). Removal measures targeting adult carp were more effective when lake areas were lower (LLA) and when there was a greater proportion of low water years (i.e., 2×10). Carp biomass density was almost always below 50 kg/ha in the LLA and 2×10 scenario.

Predicted future reductions in the area of Malheur Lake also influenced carp populations and control efforts (Figure 7). Lake area reductions of -12.5% and -25% under the no removal (No) scenario slightly decreased carp biomass density (-7% and -15% , respectively) and increased the proportion of years in which populations fell below the desired biomass threshold (16% in base scenario, 21% with -12.5% reduction, and 23% with -25% reduction). Carp removal was also more successful with decreasing lake areas in both the low water year removal (Low) and all year removal (All) scenarios. For instance,

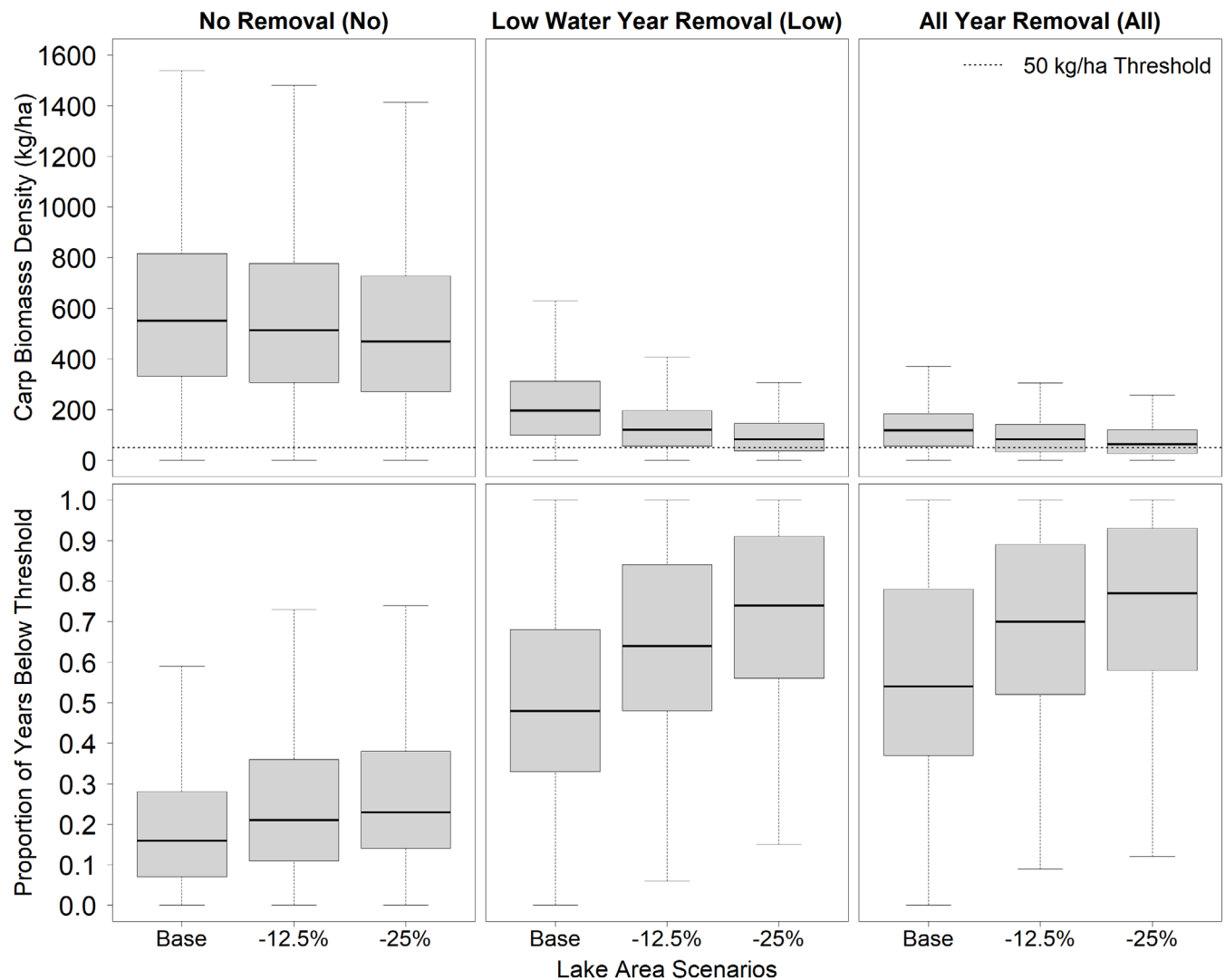


FIGURE 7 Effects of simulated future lake areas on modeled carp biomass density (top row) and the proportion of years carp density fell below the 50 kg/ha threshold (bottom row) under different carp removal scenarios: no carp removal (No; left column), low water year removal (Low; middle column), and all year removal (All; right column). Three future lake area scenarios are presented: (1) base conditions (base), (2) a 12.5% reduction in lake area (-12.5%), and (3) a 25% reduction in lake area (-25%). The base lake area scenario represents a continuation of existing lake area patterns (1938–2018), and the alternative scenarios (-12.5% and -25%) were constructed using the annual lake area output from the multiple linear regression model and subtracting 12.5% or 25% respectively, with the alternative lake areas scenarios roughly emulating published climate change predictions for the Pacific Northwest (Mote et al., 2018; Naz et al., 2016). Box-and-whisker plots incorporate the effects of interannual hydrologic fluctuations and uncertainty in model parameter values (across 10,000 model runs), where the line within each box is the median outcome, box boundaries are 25th and 75th percentiles, and whiskers are 5th and 95th percentiles

the proportion of years that the carp population fell below the 50 kg/ha threshold in the all year removal (All) scenario increased from 54% under current hydrologic conditions (base) to 77% with a 25% decrease in lake area (base –25%).

DISCUSSION

Our simulations suggest that lake area fluctuations can strongly influence carp populations and the success of carp control efforts. We found that removal efforts were generally more effective during low water years when carp are concentrated in smaller areas. The combination of these model outputs and future climate projections suggests that as systems like Malheur Lake experience increasing drought, non-native carp populations will likely decline, and the efficacy of control efforts will increase. These findings are generally applicable to shallow lake and wetland systems in which a drying/warming climate (climate change) may exacerbate lake fluctuations and thus increase the density-dependent interactions within a population of non-native carp. However, while this may be deemed a desirable outcome, prolonged dry conditions are also likely to diminish the probability of achieving desired ecological conditions (e.g., clear water, abundant submergent and emergent macrophytes, and water birds) in Malheur Lake and other carp-dominated waterbodies (Haig et al., 2019; Nielsen & Brock, 2009).

Model dynamics showed the potential for significant peaks and troughs in carp biomass density brought on by lake fluctuations. During low water years (i.e., LLA), the carp are confined to a small area, creating a peak in carp biomass density, and causing decreased recruitment and increased natural mortality (Maiztegui et al., 2019). During high water years, the carp population expands into the newly inundated area creating troughs in carp biomass, in which the population grows under weakened density-dependent conditions (i.e., low natural mortality and high recruitment). These two disparate dynamics brought on by lake fluctuations set up the scenario for boom-and-bust population growth and decline. Peaks in carp biomass density are further exacerbated in years following prolonged high water years (large lake area) because the population has more time to recover from low water events and grow under density-independent conditions. These model outputs are similar to findings of significant fluctuations in carp biomass density in other systems that experience dramatic changes in wetted area (Maiztegui et al., 2019). Although similar dynamics may be expected in Malheur Lake, direct monitoring of carp populations would be needed to confirm whether

similar fluctuations are manifested in response to lake fluctuations.

Fish species (e.g., common carp) that survive and grow best in highly variable environments are referred to as periodic strategists (large, highly fecund, and long-life span), which spread their reproductive effort, so that many years of low recruitment (low water years) are offset by high larval or juvenile survivorship when conditions are suitable (high water years; Winemiller & Rose, 1992). Periodic strategists exhibit compensatory density dependence (i.e., shifts in demographic rates), which can make these fish species resilient to perturbations, whether environmental or anthropogenic (Rose et al., 2001). For example, a study in a Midwestern lake examining the compensatory responses of carp to commercial harvest demonstrated that the survival rate of the population only decreased by 25% at an exploitation rate of 43% (Weber et al., 2016). For these reasons, periodic fish species are extremely difficult to control when they invade new systems, and control is even more challenging in highly variable environments (Rose et al., 2001).

Our results suggest that population oscillations initiated by changes in habitat area may provide opportunities for better controlling carp populations and potentially other non-native fishes. Specifically, we found that the targeting of adult carp during low water years can result in an overall lower carp biomass density with more years below the threshold whereby ecological recovery is more likely. For instance, results suggest that removing adult carp during low water years (19 years <10,000 ha) would lead to an increase in years below the desired biomass threshold; however, removing carp during all years had minimal additional benefit efforts in our simulations, suggesting diminishing returns.

Future climatic conditions in the Great Basin are expected to systematically shift over time (e.g., warming), leading to an increase in climatic and hydrologic variability (frequency, severity, and extent of droughts), with decreasing snow water equivalent throughout the 21st century (Black et al., 2018; Lute et al., 2015; Trenberth & Fasullo, 2013). These climatic changes are likely to affect many lakes, rivers, and wetlands that carp (and other non-native species) occupy. Our model analysis suggests that a drier hydrologic regime will alter the population dynamics of carp and mediate the ability of managers to control them. For instance, results suggest that reduced lake areas will decrease carp biomass density and increase the effectiveness of removal efforts. However, lower lake areas also resulted in very large, but ephemeral, peaks in carp biomass density when lake areas shifted from high to low. Additional research is needed to better understand how these extremely high but ephemeral carp densities impact aquatic ecosystems.

While model results suggest that future climatic conditions (drier) may naturally decrease carp biomass, and make populations easier to control, these same conditions may also negatively affect the aquatic ecosystem (i.e., water quality) and potentially have a greater impact than the non-native species themselves (Haig et al., 2019; Rocha et al., 2018). For instance, research has shown that increased drought conditions lead to increased turbidity, conductivity, and nutrient concentrations in shallow freshwater lakes in semiarid regions (da Costa et al., 2016; Moss et al., 2011; Rocha et al., 2018). Furthermore, specifically in the case of Malheur Lake, lake area fluctuations with an overall decrease in water availability may result in the desiccation of emergent vegetation that relies on semiannual inundation to survive and persist (Mortsch, 1998). The elimination of the remaining emergent vegetation could also make Malheur Lake more susceptible to wind suspension (increased wind fetch), enabling the wind to transfer energy into the water column, generating circular waves that extend to the sediment, suspending sediment into the water column, and ultimately increasing turbidity via (1) suspended sediment concentrations and (2) water column nutrients that promote phytoplankton productivity (Carper & Bachmann, 1984; James et al., 2004; Pearson, 2020; Scheffer & van Nes, 2007). Therefore, there are likely to be diminished returns from non-native species control in the future if the climate becomes more arid.

One element of this model that could conceivably affect our simulated carp biomass outputs is the assumption that carp are uniformly distributed throughout Malheur Lake, and thus evenly affected by population dynamics (i.e., recruitment, mortality, and adult reduction). This assumption is based on limited in situ data collected in Malheur Lake along with previous carp telemetry research conducted in the Midwestern United States. The in situ data collection effort (trap netting) demonstrated that carp are numerous and widespread in Malheur Lake, which is likely due to the large size, homogenous habitat, and uniform depths. Furthermore, previous study of carp movements demonstrated that aside from aggregations of carp during winter months and a short aggregation period in spring, carp live in small, dispersed groups in littoral habitats (Bajer et al., 2011; Penne & Pierce, 2008; AppendixS2). Thus, in a large shallow lake, with homogenous habitats and depths such as Malheur Lake (average lake area $\approx 19,600$ ha; average depth ≈ 0.58 m; max depth ≈ 1.26 m), carp are likely more uniformly distributed during the time in which the population would be most affected by the dynamics simulated herein.

Another element that could potentially affect simulated carp removal predictions is the AR and the assumption that removal rates are proportional to the area of the

lake and thus fluctuate. A sensitivity analysis demonstrated that while the model outputs are sensitive to violations of these assumptions, ultimately, we believe that in the realm of feasibility (fishing effort), the model results were fairly similar, further demonstrating that the carp population in Malheur Lake is more affected by the interactions within the population brought on by environmental fluctuations than mortality rates imposed via removal actions.

Results of this modeling work highlight the challenge of removal efforts as a means of controlling non-native fishes, such as carp. Recent reviews of control measures for non-native fishes documented a series of notable successes, but these were overwhelmingly reported from smaller and more isolated systems (Dunham et al., 2020; Rytwinski et al., 2019). Cases such as the one considered here (large-open system) represent a major challenge because effectively managing carp in the system under current conditions requires indefinite annual investments in control. Potential future conditions may improve the efficacy of carp control, but they also reduce the desired condition of the system overall (e.g., reduced extent of the lake and associated wetlands). In addition to control, physical modifications of the system itself may improve capacity to control carp. Alternatives include installation of infrastructure to manipulate lake levels or modifications of barriers within the system, allowing for greater containment of carp, and thus more efficient control (Griffiths, 1978). Such measures require very large one-time or “pulse” investments that may be more economically viable over longer planning horizons (opposed to smaller, annual “trickle” investments; Neeson et al., 2015). Managing non-native species often emphasizes early detection and control (Reaser et al., 2020), but many invaders such as carp are well established across broad extents and extremely difficult to control (Dunham et al., 2020; Lowe et al., 2000). Addressing these more familiar and widely established invaders will likely require more information-intensive assessments of the efficacy of control in changing social, economic, and climatic conditions (Güneralp & Barlas, 2003).

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