

AN ABSTRACT OF THE DISSERTATION OF

James Pearson for the degree of Doctor of Philosophy in Fisheries Science presented on May 22, 2020.

Title: Carp, Climate, and Water Quality: Applying Systems Modeling to Ecosystem Recovery in Malheur Lake, Oregon

Abstract approved: \_\_\_\_\_

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Shallow lakes exist in either a clear or turbid state, with the clear state characterized by an abundance of aquatic macrophytes, diverse aquatic biota, low water column nutrients and phytoplankton biomass, whereas the turbid state is characterized by the opposite. These two distinct states are maintained by reinforcing (positive) feedback loops that pull the system towards one of the two states. I used a mechanistic modeling approach to better understand the drivers of the currently turbid state of Malheur Lake, a large shallow lake-wetland ecosystem in southeast Oregon. Currently this system exists in a turbid state, and there has been great interest in restoring the system to a clear state by influencing two agents suspected in causing turbidity: benthic foraging by non-native carp (*Cyprinus carpio*) and wind resuspension of lakebed sediments. I began by simulating the non-native carp population in Malheur Lake and focused on controlling carp via removal efforts aimed at suppressing carp biomass below the desired 50 kg/ha threshold. These simulations indicated that individual carp removal actions would likely fail due to compensatory density dependent responses (recruitment, mortality, growth) within the carp population. Simulations further demonstrated that combinations of two or all three active removal methods could reduce the biomass below the desired threshold, however the carp reduction rate would have to be maintained  $\approx 40\%$  at each life-stage, in perpetuity. Furthermore, adding environmental fluctuations into the carp population model ultimately demonstrated that the carp population in Malheur Lake is more affected by the interactions within the population brought on by environmental fluctuations than the human capacity to impose mortality rates via removal efforts. Ultimately these results demonstrated that focusing management actions solely on the reduction of carp would likely be ineffective, and thus investigations of other mechanisms helping to maintain the turbid state was necessary. Therefore, I shifted the modeling to investigate the deleterious effects of the wind and wave energy, with simulations ultimately demonstrating that the wind-wave energy is a major driver

of the turbid state, and that restoration efforts in the form of wave reduction barriers may be used to decrease the suspended sediment concentrations and increase the water clarity. Collectively, simulation results reinforce the notion that future restoration actions in Malheur Lake must be more broadly focused (i.e. systems perspective) and guided by the principles of the alternative stable state theory.

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Carp, Climate, and Water Quality: Applying Systems Modeling to Ecosystem Recovery in Malheur  
Lake, Oregon

by  
James Pearson

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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James Pearson, Author

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TABLE OF CONTENTS	Page
Chapter 1: Introduction .....	1
References .....	6
Chapter 2: Modeling Control of Common Carp ( <i>Cyprinus Carpio</i> ) In a Shallow Lake- Wetland System .....	8
Abstract .....	9
Introduction .....	10
Methods .....	14
Study Area .....	14
Carp Population Model .....	16
Sensitivity Analysis .....	19
Carp Removal Scenarios .....	20
Results .....	22
Background Model Dynamics and Sensitivity .....	22
Active Control Scenarios .....	24
Passive Control Scenarios .....	26
Discussion .....	27
Conclusions .....	32
References .....	34
Chapter 3: Will Climate Change Inhibit or Facilitate Control of Non-native Common Carp ( <i>Cyprinus carpio</i> )? .....	43
Abstract .....	44
Introduction .....	45
Methods .....	47
Study Area .....	47
Model Description: CarpMOD1.5 .....	49
Modeling Lake Area .....	51
Carp Removal .....	53
Carp Model Scenarios .....	54
Results .....	56
Modeling Lake Area .....	56
Carp Model Scenarios .....	56
Future Hydrologic Variability: Fluctuations and Carp Removal Scenarios .....	60
Discussion .....	62

TABLE OF CONTENTS (CONTINUED)	Page
References .....	66
Chapter 4: A Spatially Explicit Sediment Resuspension Model to Evaluate Physical Controls on Clear and Turbid States in a Large-Shallow Lake Ecosystem .....	73
Abstract .....	74
Introduction .....	75
Methods .....	78
Study Area .....	78
Data Collection .....	79
Wind Resuspension Model - Assumptions .....	80
Wind Resuspension Model - Overall .....	81
Wind Resuspension Model – Equations and Coefficients .....	82
Wind Resuspension Model - Environmental and Morphological Variables .....	84
Suspended Sediment Concentration .....	86
Model Evaluation .....	87
Model Performance .....	88
Model Application .....	89
Results .....	91
Model Performance .....	91
Model Application .....	93
Discussion .....	97
References .....	104
Chapter 5: Conclusion .....	112
References .....	116



Figure 1.1. 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). .....	3
Figure 2.1. 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). .....	14
Figure. 2.2. 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. ....	17
Figure 2.3 Modeled dynamics and sensitivity of carp biomass to uncertainty in model parameter values (Table 2.2). The solid line represents the median modeled outcome and dashed lines represent the 25 <sup>th</sup> and 75 <sup>th</sup> and 5 <sup>th</sup> and 95 <sup>th</sup> percentile bounds from a global sensitivity analysis based on 10,000 simulations (see Methods). ....	23
Figure 2.4 Relative importance of different model parameters in determining carp biomass from Random Forest analysis (see Methods), ranked from most important to least important. ....	24
Figure. 2.5 Modeled carp biomass (kg/ha) resulting from single control methods (commercial harvest (Left), juvenile trapping (Center), and embryo reduction (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. ....	25
Figure 2.6 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. ...	26
Figure 2.7 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. ....	27
Figure 3.1. 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 ( $\approx 550$ ha). ....	48

Figure 3.2. Carp population dynamics were simulated under nine deterministic lake area scenarios, which represent different combinations of high and low lake areas, including three duration scenarios: 1) 6 high and 6 low (6x6; solid black line), 2) 4 high and 8 low (4x8; dashed black line), and 3) 2 high and 10 low (2x10; dashed and dotted black line) and three lake area scenarios: 1) high lake area (HLA - Max: 30,000 Min: 12,500, 2) medium lake area (MLA - Max: 25,000 Min: 7,500), and 3) low lake area (LLA - Max: 20,000 Min: 2,500). Deterministic lake simulations are overlaid on modeled lake area for 1938-2018..... 55

Figure 3.3. Simulated median carp biomass (kg/ha) of 10,000 model runs per removal scenario (NR, LWYR, AYR), using historical lake levels (1938-2018). Solid black line is the carp biomass under the no removal (NR) scenarios, black dashed line is the carp biomass under the low water year removal (LWYR) scenario (<10,000 ha), and black dotted line is the carp biomass under the all year removal (AYR) scenario. .... 57

Figure 3.4. Left: Median carp biomass (kg/ha) outputs using the historical lake area (1938-2018) under the three individual removal scenarios (NR, LWYR, and AYR). Right: Median proportion of years for which the carp biomass fell below the designated threshold under each removal scenario using historical lake areas. Box-and-whisker plots demonstrating the sensitivity of modeled outputs to uncertainty in model parameter values. The bold black lines within each box are the median outputs, outer edges of box are 0.25 and 0.75 quantiles, and outer whiskers are 0.05 and 0.95 quantiles. .... 58

Figure 3.5. Median modeled carp biomass (kg/ha) outputs for the 10,000 model runs for each lake area scenario. The solid black line represents no removal (NR) and the dashed black line represents all year removal (AYR) of carp. The graphical columns represent the three hydrologic lake area categories (HLA – high lake area, MLA – medium lake area, LLA – low lake area), while the graphical rows represent three duration scenarios: 1) 6 high and 6 low (6x6), 2) 4 high and 8 low (4x8), and 3) 2 high and 10 low (2x10; Figure 3.2; see Methods). The low water year removal (LWYR) scenario was left out because they demonstrate a similar response with slightly higher peaks due to removal only during low years (describe in more detail in discussion)..... 59

Figure 3.6. Modeled carp population outputs with simulated declines in lake area of Malheur Lake. The graphs in the left column were simulated using the base (contemporary lake areas) scenario, the graphs in the center column are the base hydrologic scenario with a 12.5% reduction in lake area, and the graphs on the right are a 25% reduction. The top row of graphs displays the mean carp biomass (kg/ha) under the three carp reduction scenarios (NR – No Removal, LWYR – Low Water Year Removal, AYR – All Years Removal). The bottom row of graphs displays the average proportion of years in which carp biomass falls below the 50 kg/ha threshold. Box-and-whisker plots display sensitivity in modeled values to uncertainty in both hydrologic fluctuations and uncertainty in model parameter values. 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. .... 61

Figure 4.1. Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The dark gray region depicts the lake area at 1248.75 m (3,663 ha), the medium gray region depicts the lake area at 1248.25 m (11,071 ha), and the light gray region depicts the lake area at 1247.75 m (19,952 ha; average fall lake area  $\approx$  19,600 ha)..... 79

Figure 4.2. The graph on the left demonstrates how the two sites in Malheur Lake (NE and SE Sites;  $\approx 4.4$  km apart) respond similarly over long time scales (April 28<sup>th</sup> – October 15<sup>th</sup>) and the graph on the right demonstrates how these same sites also respond similarly to events on shorter time scales (August 19<sup>th</sup> – August 26<sup>th</sup>). ..... 81

Figure 4.3. Conceptual diagram of the wind resuspension model. The thin black lines denote the input locations of the model parameters (text) into the nine governing equations (blue circles), the thin red lines denote the flow of values through the model, the valves (large blue arrows) depict flow of sediment into or out of the water column, and the boxes (blue) represents the suspended sediment concentration (SSC; mg/L) in the water column. The SSC is made up of two distinct fractions of sediment (i.e. heavier particles (heavy) and lighter particles (light)). ..... 82

Figure 4.4. Graphical display demonstrating the three distinct fractions that make up the suspended sediment concentration (SSC; mg/L) in the water column. The green line denotes a phytoplankton fraction (derived via stoichiometry, Tamara Wood, U.S. Geological Survey, Oregon Water Science Center, unpublished data), the brown line denotes a lighter fraction (slow to fall out of suspension), and the black line denotes the heavier fraction of the SSC (quick to fall out of suspension). ..... 87

Figure 4.5. Wind speed and wind direction during the 2018 baseline model simulation. The graph on the left is a wind rose that demonstrates the predominant wind direction and the graph on the right demonstrated the wind speed over the simulated time period. The data used in this simulation was collected at the permanent USGS meteorological station on the northwest shoreline of Malheur Lake (30 minute intervals: March 1<sup>st</sup> – November 30<sup>th</sup>). ..... 90

Figure 4.6. Model calibrations and validations for both sites over all three years of data collection. The black lines denote the continuous suspended sediment concentration (SSC; mg/L) data collected in Malheur Lake during the three sampling years at two separate locations (NE and SE sites). The blue line denotes the individually calibrated models (heavy and light) while the red lines denote the corroborated model outputs. The 2017 calibration was simulated using data collected August 31<sup>st</sup> – November 7<sup>th</sup>, the 2018 calibration was simulated using data collected April 20<sup>th</sup> – August 1<sup>st</sup>, 2019 calibration and validation was simulated using data collected April 28<sup>th</sup> – October 15<sup>th</sup>. ..... 92

Figure 4.7. Heuristic model outputs demonstrating the forces exerted along the sediment (bottom shear stress ( $\tau$ ); N/m<sup>2</sup>) at different depths (0.25 – 1.0 m), wind fetches (0 – 10,000 m), and wind speeds (2 - 12 m/s). ..... 94

Figure 4.8. Maps demonstrating the average suspended sediment concentration (SSC; mg/L) for each cell throughout Malheur Lake at the three distinct lake elevations (1247.75, 1248.25, 1248.75; Table 4.3). ..... 95

Figure 4.9 Maps demonstrating the reduction in the average suspended sediment concentration (SSC; mg/L) due to the implementation of WRB. The collection of maps in the top area display how the overall SSC is effected by WRB at similar lake elevations (1248.25 m). The collection of maps in the bottom area display the overall change in SSC brought about by 6 WRB implemented at three different lake elevation (1247.75, 1248.25, 1248.75 m). ..... 96

## LIST OF TABLES

Page

Table 2.1. Equations used in CarpMOD to simulate the population dynamics of carp in Malheur Lake (Appendix A) .....	19
Table 2.2 Values of CarpMOD parameters included in the global sensitivity analysis.....	19
Table 3.1 Equations used in CarpMOD1.5 to simulate the population dynamics of carp in Malheur Lake .....	51
Table 3.2 Values for the CarpMOD1.5 parameters. ....	51
Table 3.3. Malheur Lake fluctuation model variables. ....	53
Table 4.1. Values of model parameters with the letters <i>H</i> and <i>L</i> denoting parameters calibrated to simulate the heavier and lighter sediment fraction respectively. ....	84
Table 4.2. Model calibration and validation results. The two distinct erosion-deposition modules (heavy and light) were individually calibrated using the continuous 2019 suspended sediment concentration (SSC; mg/L) with the data separated into two distinct fractions (heavy and light). The overall model was then corroborated using the additive outputs from the two erosion-deposition model against data from 2017-2019 at both sites (NE and SE Sites).....	93
Table 4.3. Table displaying simulation outputs for the wave reduction barriers (WRB) scenarios. Table A demonstrates the average suspended sediment concentration (SSC; mg/L) concentration overall average SSC for each lake elevation and WRB scenarios. Table B demonstrates the average percent change per cell in comparison to the baseline model. Table C demonstrates the average percent change per cell per WRB. The conditional formatting in each table is meant to more easily identify the higher (red) and lower (blue) values.....	97
Table 4.4 Comparison of wind resuspension parameters. ....	104

LIST OF APPENDICIES	Page
Appendix A: CarpMOD - Population Dynamics Model Equations and Parameters .....	118
State Variable Equations.....	118
Von Bertlanffy Growth Model.....	118
Length-Weight Relationship .....	119
Probability of Maturity .....	119
Ricker Recruitment Equation.....	120
Annual Natural Mortality.....	120
Appendix B: Modeled Avian Piscivory .....	122
Appendix C: Basic Hydrologic Model.....	125

## **Chapter 1: Introduction**

Freshwater ecosystems occupy  $\approx 0.8\%$  of the Earth's surface and support  $\approx 125,000$  species (9.5% of described species), including a third of all vertebrates and provide irreplaceable economic, cultural, aesthetic, scientific, and educational value (Dudgeon et al., 2006; Balian et al., 2008; Strayer & Dudgeon, 2010). Due to their importance to both humans and ecosystems alike, there is a need to restore degraded freshwaters. Although well-intentioned, restoration efforts are by nature reactive and often implemented without a full understanding of the major forces driving the system (Hobbs et al., 2011). Therefore, to better understand the process, flow, and feedbacks in a system, researchers often use ecological and physical models prior to intervention to elucidate these interconnections, which are often complex and counter intuitive (Scheffer et al., 1993; Janse, 1997; Chung et al., 2009). Here I address these issues in the context of restoring a shallow lake ecosystem.

A major focus of research into the ecology of shallow lakes is on processes that determine if they exist in one of two alternative stable states, clear or turbid. The clear state is characterized by an abundance of aquatic macrophytes, diverse aquatic biota, low water column nutrients and phytoplankton biomass, whereas the turbid state is characterized by the opposite (Scheffer et al., 1993; Scheffer & Carpenter, 2003; Janssen et al., 2014). A shift from a clear to a turbid state can be induced by several physical or ecological factors, and interactions among them, including climatic drivers, nutrient fluxes, hydrologic variability, biotic invaders, and losses of native species. These factors can also increase the system's resistance to a shift between states via reinforcing feedbacks (Hargeby et al., 2004). Identifying the mechanisms that maintain the turbid state and determining how to effectively reduce their deleterious impacts on a shallow lake via restoration activities is a critical step in eventually shifting a lake back to the clear state. In this dissertation, I explicitly investigated two mechanisms that can drive turbid states in shallow lakes: non-native Common Carp (*Cyprinus carpio*) and wind-driven sediment resuspension.

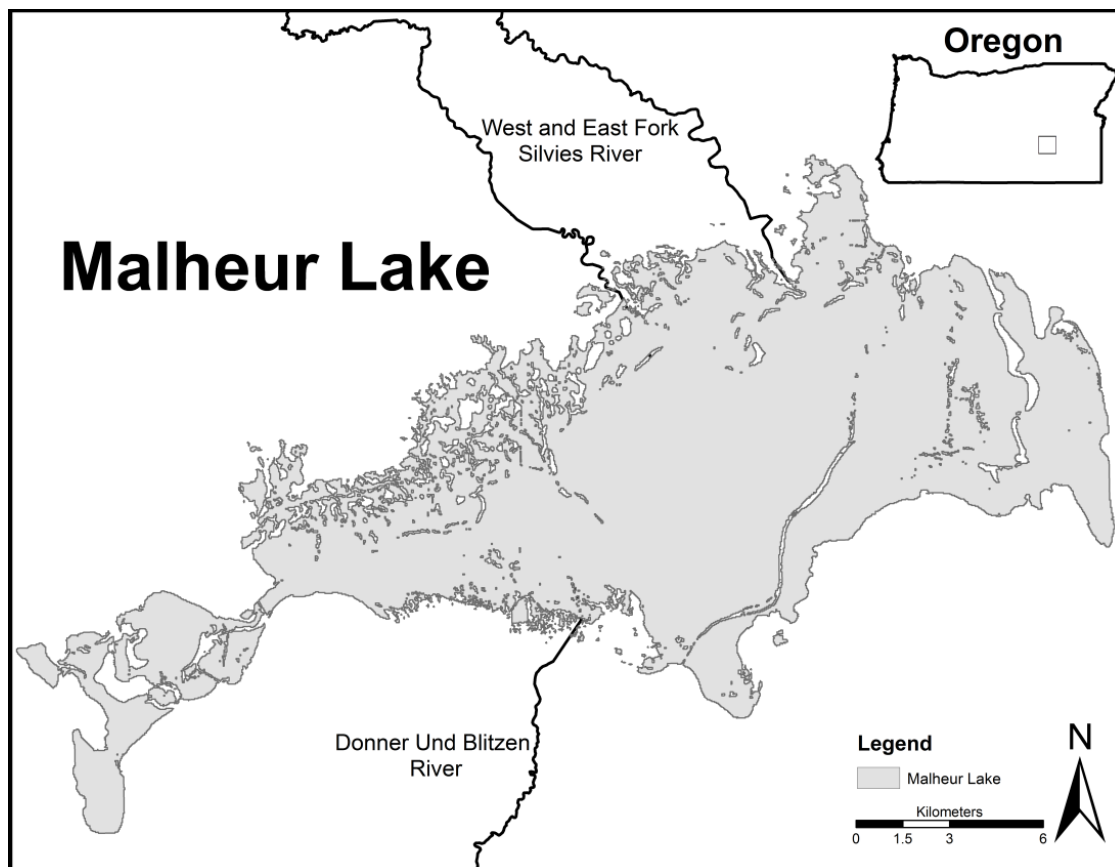


Figure 1.1. Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The gray shaded region depicts the long-term average lake area ( $\approx 14,000$  ha).

I focused my work on Malheur Lake, a major wetland-lake system in southeast Oregon that is currently the focus of many restoration activities. Malheur Lake is a large ( $\approx 19,600$  ha), shallow (average depth  $\approx 0.58$  m; max depth  $\approx 1.26$  m), polymictic, terminal lake (endorheic basin), located in Southeastern Oregon, with two major freshwater inputs, the Silvies and Donner und Blitzen Rivers (Miller, 2012; Williams et al., 2014). Malheur Lake is located within the Malheur National Wildlife Refuge (MNWR), which was established by President Theodore Roosevelt in 1908, and is managed by the U.S. Fish and Wildlife Service (USFWS). Malheur Lake was once one of the largest freshwater marshes in North America, serving as an important breeding and migration area for migratory ducks and geese, breeding area for



numerous shorebird species, and habitat for resident species (Duebbert, 1969; Cornely, 1982; MNWR, 2012). Currently, the aquatic ecosystem of Malheur Lake is a highly turbid environment, with a lack of submergent and emergent vegetation, high levels of nutrients and suspended sediments, and diminished fish assemblage dominated by the non-native benthivorous Common Carp (*Cyprinus carpio*; hereafter carp).

While both carp and wind driven sediment resuspension may be drivers of the turbid state in Malheur Lake, the carp are often most focused on by managers because they are an easily identifiable problem, with an intuitively straightforward solution (i.e. reduce or eradicate the species). Carp can have an adverse effect on the aquatic ecosystem through their activity and mode of feeding, in which the carp use a suction feeding technique known as crossflow filtration that captures benthic macroinvertebrates and expels sediment via the opercular slits (Callan & Sanderson, 2003). This mode of feeding leads to a reduction in benthic invertebrate abundance, diversity, and richness, physically uproots aquatic vegetation, and suspends sediment and nutrients into the water column (Miller & Crowl, 2006; Weber & Brown 2009; Weber et al., 2011). These impacts, along with the excretion of nutrients (Morgan & Hicks, 2013), lead to an increase in suspended sediments and phytoplankton biomass and thus overall turbidity (Breukelaar et al., 1994; Lougheed et al., 1998), which diminishes light availability, and further inhibits the growth of aquatic vegetation (Weber et al., 2011).

Biologists at MNWR have undertaken several large-scale carp removals, including eight rotenone (piscicide) treatments removing a total of 2.5 million carp (Miller, 2012). Effectiveness monitoring conducted in the years following the rotenone treatments determined that submergent vegetation and waterfowl production rebounded. This apparent success was short lived, however, with the aquatic ecosystem of Malheur Lake quickly returning to the turbid state (Ivey et al., 1998). While rotenone treatments have been successful at quickly reducing

the carp population and promoting short term increases in the aquatic health of Malheur Lake (e.g., increases in submergent vegetation and waterfowl production; Ivey et al., 1998), rotenone treatments have failed to suppress carp across years, and recovery of carp is hypothesized to be the reason for the quick rebound in the turbid state. Furthermore, a review of the carp literature established that impacts from carp can potentially be reversed if the overall carp biomass is maintained below 50 kg/ha (Vilizzi et al., 2015). Therefore, it is paramount to investigate the potential efficacy of carp control efforts targeted at not only reducing the carp population, but maintaining the suppression in perpetuity.

My dissertation is organized into three main chapters exploring the mechanisms that influence a shift between the turbid and clear state in Malheur Lake. In Chapter 2, I constructed a carp population dynamics model (CarpMOD), which enabled me to determine the efficacy of control efforts targeted at multiple life stages (embryos, juveniles and adults) via both active and passive removal efforts. In Chapter 3, I modified the original carp population model (CarpMOD) to incorporate hydrologic variability (CarpMOD1.5), which allowed the simulation of past and future hydrologic scenarios, thus enabling me to understand how lake fluctuations may affect the carp population as well as our ability to effect the population via removal efforts. In Chapter 4, I constructed a spatially explicit one-dimensional wind resuspension model, which enabled me to investigate variations in suspended sediment concentrations in response to environmental and morphological drivers (i.e. wind speed, wind fetch and water depths). In my final chapter, I integrate the findings of Chapters 2, 3, and 4 to broadly discuss the reinforcing feedback loops pulling Malheur Lake towards the turbid state, and describe how these loops may be overcome via restoration efforts to restore Malheur Lake back to the clear state. Collectively, the results from the studies described herein demonstrate the need for restoration efforts in Malheur Lake to be broadened beyond merely removing carp to include managing the multiple drivers of the turbid state.

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## Chapter 2: Modeling Control of Common Carp (*Cyprinus Carpio*) In a Shallow Lake-Wetland System<sup>1</sup>

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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 the non-native 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.

## **Introduction**

Shallow lakes and wetland ecosystems are among some of the most important habitats on Earth due to their numerous ecological functions, such as groundwater 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; Scheffer et al., 1993; Güneralp & 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 & 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, 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; Smith, 1896; Cole, 1905; Nico & 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 & Brown 2009; Bajer & 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 & Hirsch, 2015). Benthic foraging uproots aquatic vegetation while simultaneously suspending sediment in the water column, which increases turbidity and diminishes light penetration (Weber & 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 & 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 & 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 & Walker, 2004; Weber & Brown 2009; Colvin et al., 2012b; Brown & 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 & 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 & 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 & Kimmel, 1990; Dwyer et al., 1993; Dwyer et al., 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  $\geq 20$  V/cm as well as Goldfish (*Carassius auratus*) when exposed to  $\geq 16$  V/cm (Natile 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. = 1248.75 m; Figure 2.1), 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  $\approx 0.58$  m; max depth  $\approx 1.26$  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  $\approx 7,770$  km<sup>2</sup> (Miller, 2012; Williams et al., 2014). During the period 1975 to 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).

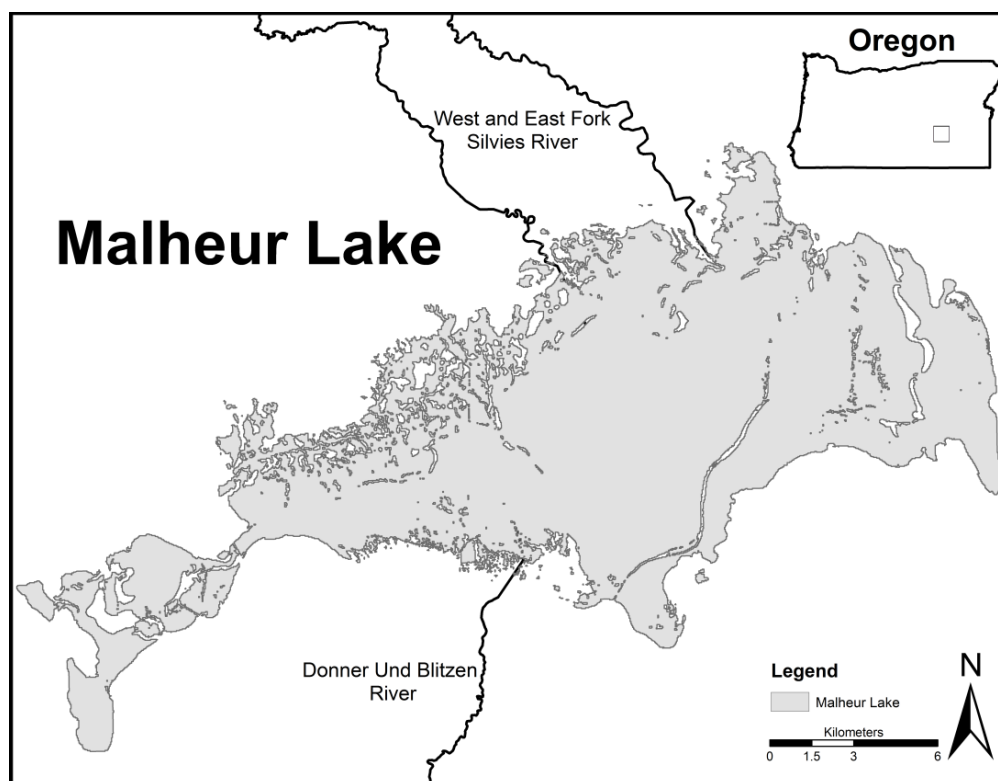


Figure 2.1. Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The gray shaded region depicts the long-term average lake area ( $\approx 14,000$  ha).

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 (*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 Silvies 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 USA<sup>2</sup>), and is a modified version of CarpSIM (Brown & Walker, 2004; Brown & 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 success is based on a density-dependent recruitment relationship between the density ( $\text{ha}^{-1}$ ) of spawning adults and the subsequent juvenile recruits (age 0; Figure 2.2; Ricker, 1954; Harris & Gehrke, 1997; Koehn et al., 2000; Brown & 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 ( $< \text{age } 4$ ) is increased due to avian predation as a function of the population size and annual consumption rates of avian piscivores (Appendix A; Wiens & 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 & Neumann, 1996; Schneider et al., 2000; Jackson et al., 2008). Further description of the major equations used in CarpMOD are presented in Appendix

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<sup>2</sup> 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.

A. 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 ( $DT=1$ ) using Euler's numerical integration method, initiated with 500 age 1 carp, and ran for 100 years.

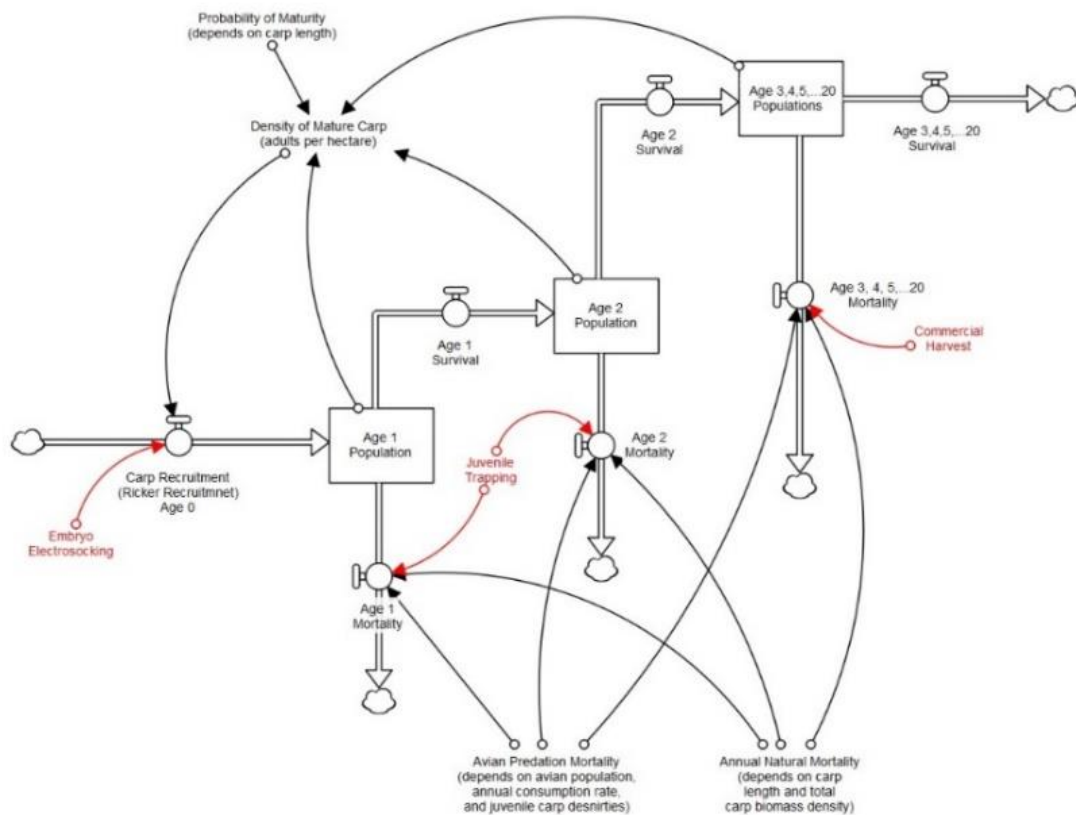


Figure. 2.2. Conceptual Model of the carp population model. Boxes represent stocks of carp in each age class (from age 1 to age 20); valves (white arrows) depict flow of carp from one age to the next, recruitment, and mortality; small black arrows denote causal relationships between model components; and small red arrows represent active control measure imposed on the carp population.

The five major equations used in CarpMOD are displayed in Table 2.1 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,  $L_{\infty}$  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  $\rho_i$  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 ( $\alpha$ ), and a density-dependent coefficient ( $\beta$ ) 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 re-calculated 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 B (Wiens & Scott, 1975; Roby et al., 2003).

<sup>3</sup>Table 0.1. Equations used in CarpMOD to simulate the population dynamics of carp in Malheur Lake (Appendix A)

Model component	Equation	Reference
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	$\rho_i = (1 + e^{\ln((19)(L_{(A)} - LM50)/(LM50 - LM95))})^{-1}$	Brown & Walker, 2004
Ricker Recruitment	$R = a * S * \exp(-\beta * S) \cdot (1 - EE_R)$	Ricker, 1954; Brown & Walker, 2004
Annual Natural Mortality (Age 1 & Age 2)	$V_{(A)} = (1 - e^{-0.06(\frac{L_{(A)}}{L_{\infty}})^{-1.5}} + 10^{-4} \cdot D) \cdot (1 - JT_R)$	Charnov et al., 2013; Bajer et al., 2015
Annual Natural Mortality (Age 3+)	$V_{(A)} = (1 - e^{-0.06(\frac{L_{(A)}}{L_{\infty}})^{-1.5}} + 10^{-4} \cdot D) \cdot (1 - CH_R)$	Charnov et al., 2013; Bajer et al., 2015

Table 0.2 Values of CarpMOD parameters included in the global sensitivity analysis

Parameters	Symbol	Function	Mean	Variance	Reference
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.	$L_{\infty}$	VBGM	818.02754	41.3931	Derived via data from Malheur Lake
Alpha Coefficient	$\alpha$	Recruitment	20.0825	16.1242	Brown & Walker, 2004; Brown & Gilligan, 2014
Beta Coefficient	$\beta$	Recruitment	0.0162	0.0039	Brown & Walker, 2004; Brown & Gilligan, 2014
Len. of Maturity 50	LM50	Maturity	309.667	31.754	Brown & Walker, 2004; Brown & Gilligan, 2014
Len. of Maturity 95	LM95	Maturity	364.667	47.343	Brown & Walker, 2004; Brown & Gilligan, 2014

## 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 2.2). For each simulation, the values for each parameter were selected from a normal distribution, either

<sup>3</sup> Table 2.1. The Von Bertalanffy's growth model (VBGM) equation consists of  $L_{(A)}$  which is the length of the carp at age,  $L_{\infty}$  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  $\rho_i$  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,  $\alpha$  is the density-independent coefficient,  $\beta$  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  $A$ ,  $L_{\infty}$  is the asymptotic average length (mm) of the carp population,  $D$  is the density of age-1 + carp (kg/ha),  $JT_R$  is the the juvenile trapping rate, and  $CH_R$  is the commercial harvest rate (Charnov et al., 2013; Bajer et al., 2015).



using data from Malheur Lake, or literature sources (Table 2.2). 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 & 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 & 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 2.1). Juvenile trapping simulates the removals of carp ages 1 and 2 ( $\approx 151$  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 2.1). Commercial harvest affects carp age 3+ (Age 3  $\approx$  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 2.1).

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, 2013<sup>4</sup>), which is

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<sup>4</sup> Available online: [https://www.fws.gov/refuge/Malheur/what\\_we\\_do/conservation.html](https://www.fws.gov/refuge/Malheur/what_we_do/conservation.html)

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 (Figure 2.3), 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  $\approx 5.8$  kg/ha of age 1+ ( $\geq 1$  years old) carp annually. Furthermore, the model predicted a natural (density-dependent) mortality rate of  $\approx 0.57$  for age 1 individuals, which is similar to that reported in other studies (Bajer et al., 2015; Osborne, 2012).

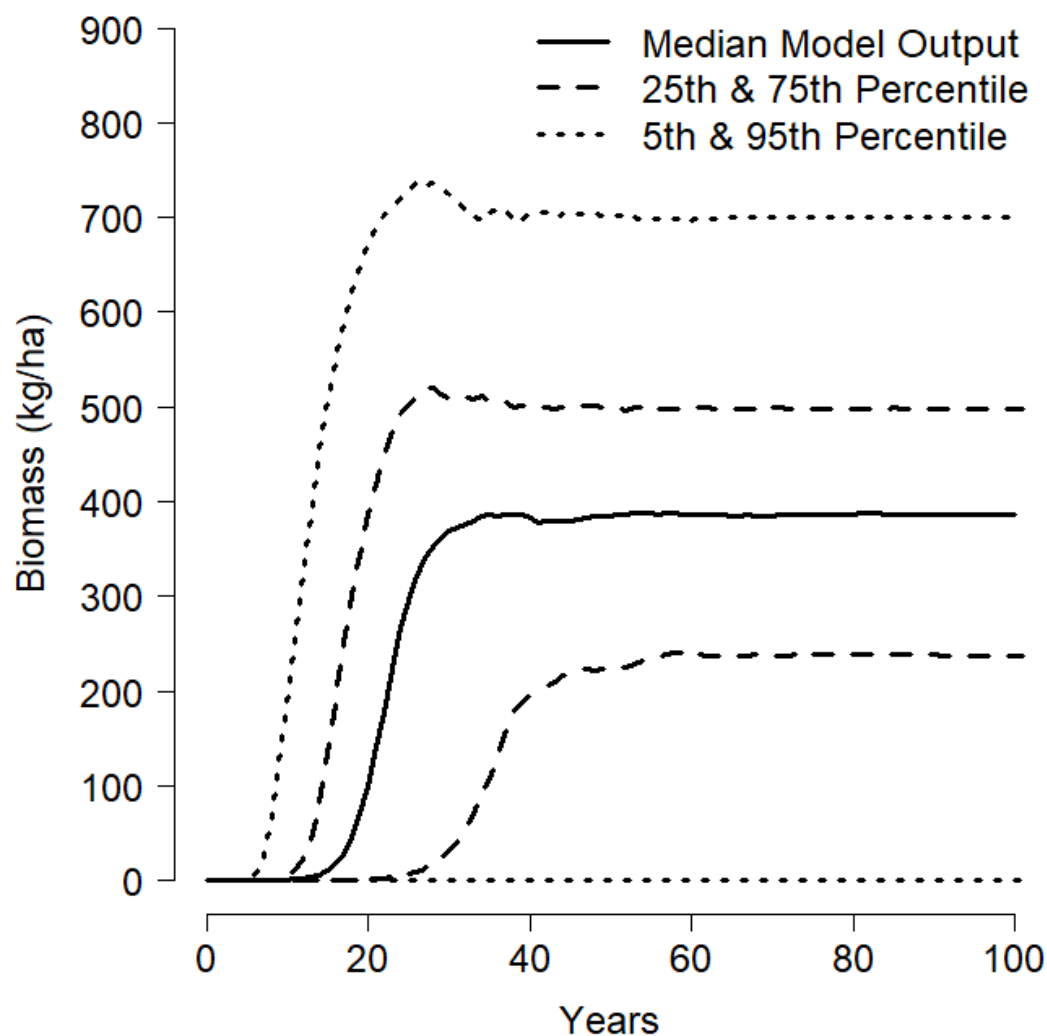


Figure 2.3 Modeled dynamics and sensitivity of carp biomass to uncertainty in model parameter values (Table 2.2). The solid line represents the median modeled outcome and dashed lines represent the 25<sup>th</sup> and 75<sup>th</sup> and 5<sup>th</sup> and 95<sup>th</sup> percentile bounds from a global sensitivity analysis based on 10,000 simulations (see Methods).

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; Figure 2.3). 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 ( $\alpha$  Recruitment Coefficient  $\approx$  52.0% and  $\beta$  Recruitment Coefficient  $\approx$

16.8%) and the length at age relationship (Growth Coefficient ( $k$ )  $\approx$  16.3%; Figure 2.4). The relatively large uncertainty attributed to the  $\alpha$  Recruitment Coefficient and  $\beta$  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 & Walker, 2004; Brown & Gilligan, 2014; Table 2.2; Figure 2.3). 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.

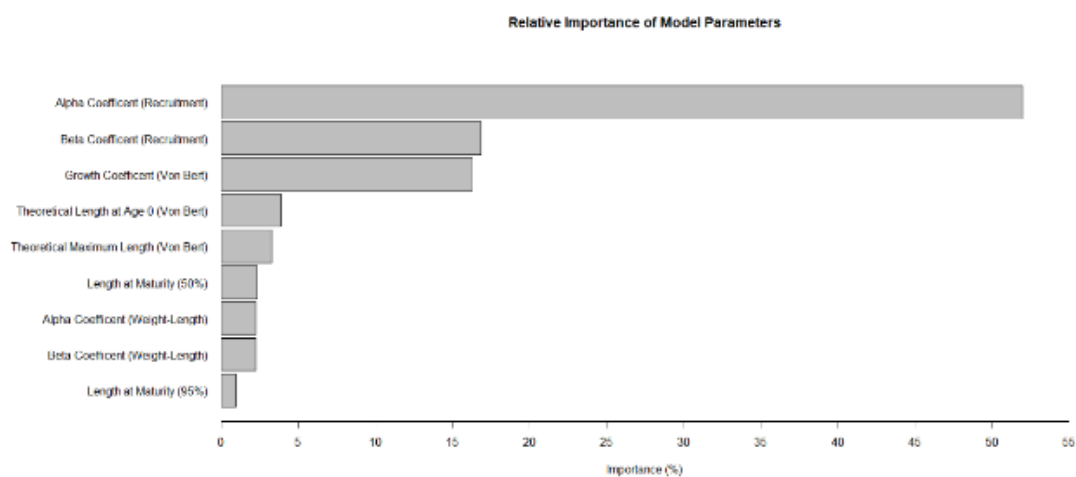


Figure 2.4 Relative importance of different model parameters in determining carp biomass from Random Forest analysis (see Methods), ranked from most important to least important.

### 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 ( $< 50\text{kg/ha}$ ; Figure 2.5-2.6). Due to the collective influences of uncertainties surrounding model parameters (Table 2.2), however, there were always a few instances where any level of control resulted in a reduction of the carp biomass below the desired threshold ( $< 50\text{kg/ha}$ ; Figure 2.5-2.6). 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).

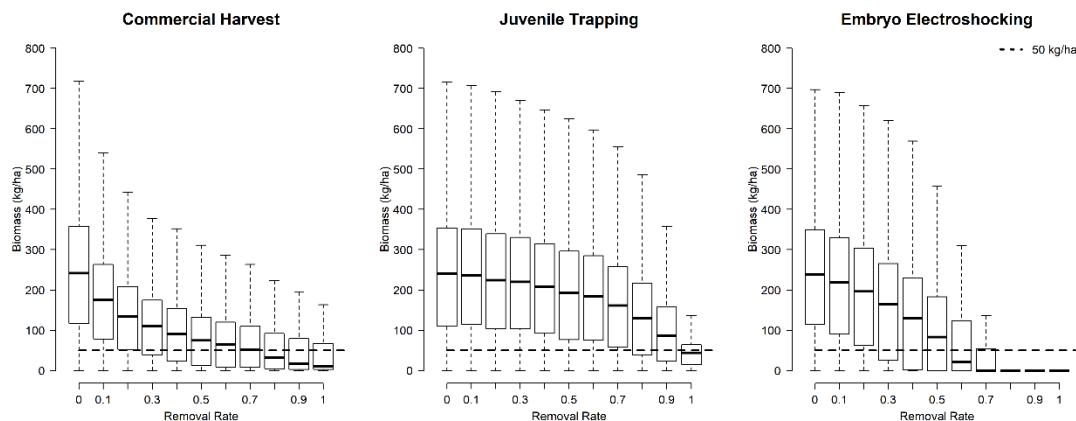


Figure 2.5 Modeled carp biomass (kg/ha) resulting from single control methods (commercial harvest (Left), juvenile trapping (Center), and embryo reduction (Right)). Box-and-whisker plot were constructed utilizing the final simulated carp biomass (year 100), and demonstrate the sensitivity of modeled 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.

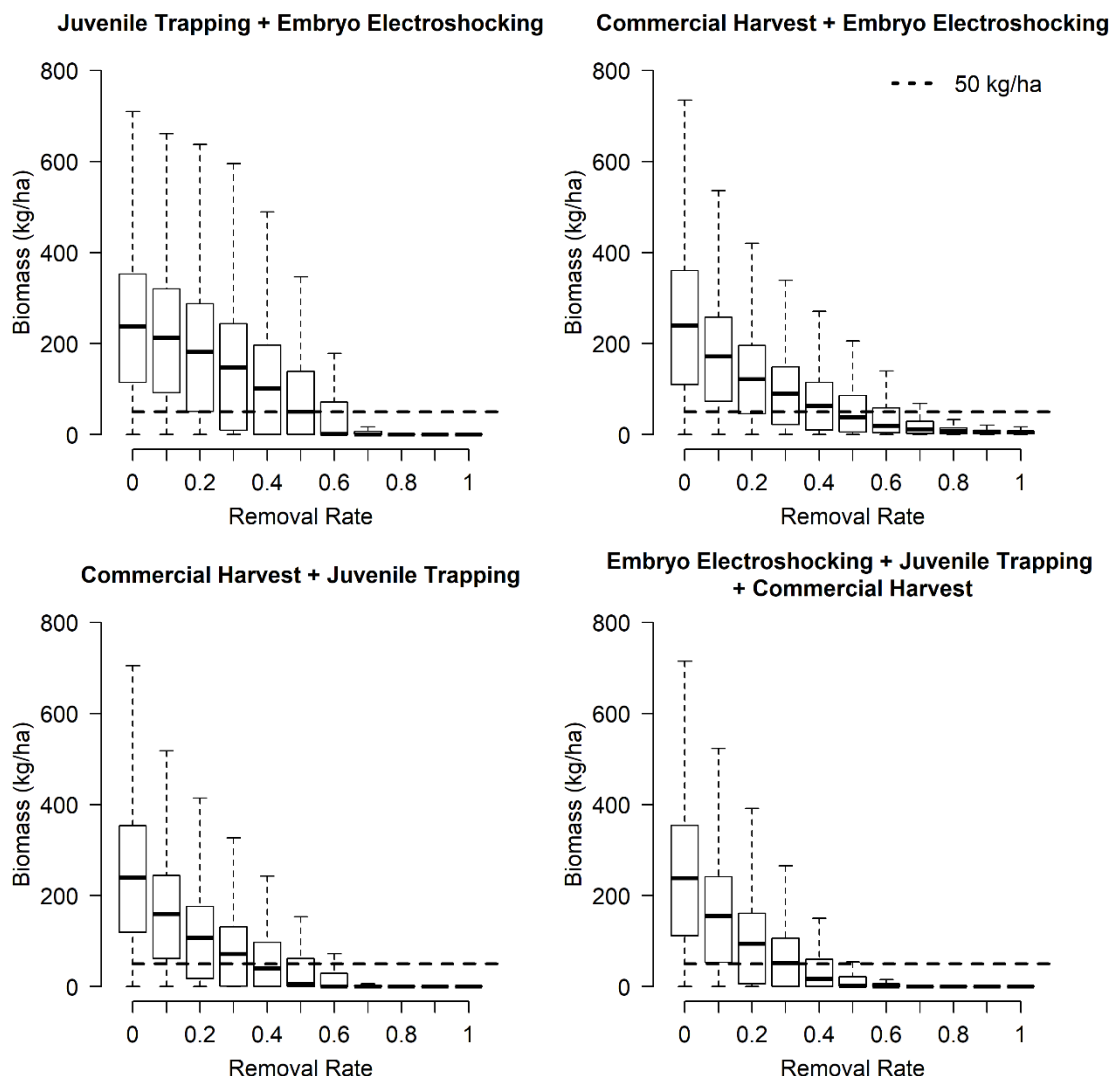
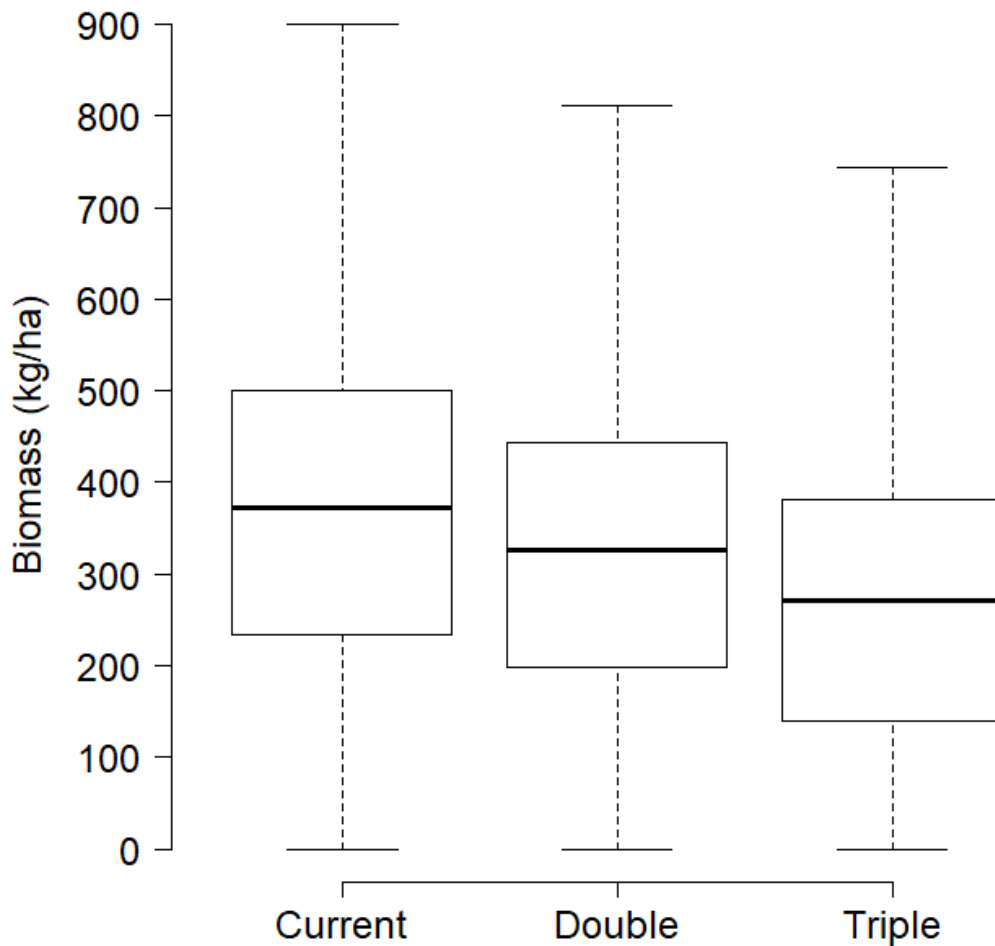


Figure 2.6 Results for combinations of control methods (embryo electroshocking and juvenile trapping (Top-Left), commercial harvest and juvenile trapping (Top-Right), commercial harvest and embryo electroshocking (Bottom-Left), and all methods in combination (Bottom-Right)). Box-and-whisker plot were 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.

### 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; Figure 2.7). 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.



### Avian Piscivore Populations

Figure 2.7 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.

### 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 & 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 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 & Walker, 2004; Brown & Gilligan, 2014; Lechelt & 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 (Figure 2.6). 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; Simpson et al., 2018). Prior to this 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 & Parisch, 1993; Penne & 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 ( $\approx 69$  hours) 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 & 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 (Figure 2.7). 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 kg/ha was predicted, however when the avian piscivore populations were doubled and tripled the model predicted a non-mature biomass of 33 and 36 kg/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 kg/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 kg/ha, phosphorus 295 kg/ha, turbidity 256 kg/ha), vegetation (phytoplankton 160 kg/ha and aquatic macrophytes 204 kg/ha), invertebrates (zooplankton 114 kg/ha), and vertebrates (fish 100 kg/ha and waterfowl 50 kg/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 & Walker, 2004; Weber et al., 2011; Colvin et al., 2012b; Brown & Gilligan, 2014; Lechelt & 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, 1997; Weber & Brown, 2013; Weber et al., 2016). In these instances, our findings support those of other studies (Weber & Brown 2009; Lechelt & 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 & 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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### **Chapter 3: Will Climate Change Inhibit or Facilitate Control of Non-native Common Carp (*Cyprinus carpio*)?**

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## **Abstract**

Non-native Common Carp (*Cyprinus carpio*; hereafter referred to as “carp”) have been implicated in the decline of aquatic health in water bodies worldwide. A capacity for rapid population growth makes carp a difficult species to control. Research on carp is often focused on direct control and the ability to quickly suppress carp biomass below a desired threshold. However, lake fluctuations likely influence the potential outcomes of control efforts. To investigate how these factors interact we employed a modified version of an age-based population model (CarpMOD1.5) to investigate how hydrologic variability (lake area) may influence the dynamics and efficacy of carp control. We simulated three scenarios: 1) no carp removal, 2) carp removal during low water years, and 3) carp removal during all years. Results of these simulations suggest that environmental variability in the form of lake area fluctuation strongly controls carp population dynamics and that no individual control scenario consistently reduces the carp biomass below the targeted threshold (50 kg/ha). Simulations further demonstrated that increasing efforts via carp removal actions during low water years to carp removal actions every year only led to a minimal further reduction in the overall carp biomass. These results derive from two factors: 1) density dependent interactions within the carp population and 2) decreased removal efficiencies during high water years. Ultimately, simulations demonstrated 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 efforts.

## **Introduction**

Humans have altered freshwater ecosystems directly via water pollution, flow modification, degradation of habitat, fisheries overexploitation, and introduction of non-native species, and indirectly via anthropogenic climate change that has led to increased water temperatures, altered stream flow patterns, decreased duration of ice cover, and increased storm events (Ashizawa & Cole, 1994; Poff et al., 2002; Strayer & Dudgeon, 2010). Individually, these alterations have had negative impacts on endemic species and biodiversity (Dudgeon et al., 2006; Dudgeon, 2010), but cumulative effects resulting from interactions among these factors are also important. An example is the interactions between climate change and the spread of non-native species, which together is an urgent threat to global freshwater biodiversity (Perrings et al., 2000; Roy, et al., 2014; Hellmann et al., 2008). 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. 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). Therefore, understanding how climate change will influence efforts to control non-native species is of great importance to freshwater ecosystem management.

Common Carp (*Cyprinus carpio*) are 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 (Harris & Gehrke, 1997; Britton et al., 2007; Pietsch & Hirsch, 2015). Once Common Carp (hereafter “carp”) are found in a novel habitat, managers frequently implement control strategies to halt further spread and control population size (Sakai et al., 2001; Lodge et al., 2006). Control strategies that target the adult life stage have 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 et al., 2009). These seemingly counterintuitive responses are likely a consequence of positive and negative feedback loops that control carp population dynamics. For instance, carp exhibit strong density dependence in which demographic rates (i.e. mortality, growth, and recruitment) shift in response to variations in the population's overall density, thus, making carp resilient to perturbations—including population control efforts (Healey, 1980; Rose et al., 2001; 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. Colvin et al., 2012; Brown & Gilligan, 2014; 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 variable natural environmental conditions (Colvin et al., 2012; Brown & Gilligan, 2014; 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). Therefore, there is a need to link population models to environmental fluctuations to better understand how a changing climate may affect the population dynamics and carp control efforts.

Understanding the effects of environmental fluctuations on the ability to control a non-native species such as carp is important because background fluctuations are being altered by a changing climate (Reidmiller et al., 2017). In many of the freshwater ecosystems where carp

have invaded, climate change is altering hydrologic regimes, which influence the frequency and magnitude of high and low water levels (Poff et al., 1997). For instance, in the Great Basin region of the United States—where many lakes have been invaded by carp—climate change projections predict a decrease in the annual snow water equivalent, and more frequent drought conditions (low spring snowpack; Lute et al., 2015; Dalton et al., 2018; Mote et al., 2018; Snyder et al., 2019), which in turn, is likely to reduce the size of lakes, rivers and wetlands that carp occupy.

In this study, we adopted a system dynamics 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 three questions: (1) how do natural fluctuations in lake area influence carp population biomass; (2) how do lake fluctuations affect population control efforts; and (3) how might alterations to lake area with climate change influence carp abundance 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 the natural hydrologic cycles and potential future climatic variation: information that can be used by managers when attempting to control carp in locations that have a highly variable hydrologic environment.

## **Methods**

### **Study Area**

Our study system was Malheur Lake (elev. = 1248.75 m), a large (average  $\approx$  19,600 ha), shallow (average depth  $\approx$  0.58 m; max depth  $\approx$  1.26 m), terminal lake (endorheic basin) located within the Malheur National Wildlife Refuge (MNWR) in the Great Basin of Southeastern

Oregon (Lat: 43.3115 and 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 3.1). The fluctuations in lake area are primarily driven by precipitation runoff and evapotranspiration (Hubbard, 1975; Hamilton et al., 1986). 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 Rivers, which drain a total area of  $\approx 7,770 \text{ km}^2$  (Miller, 2012; Williams et al., 2014).

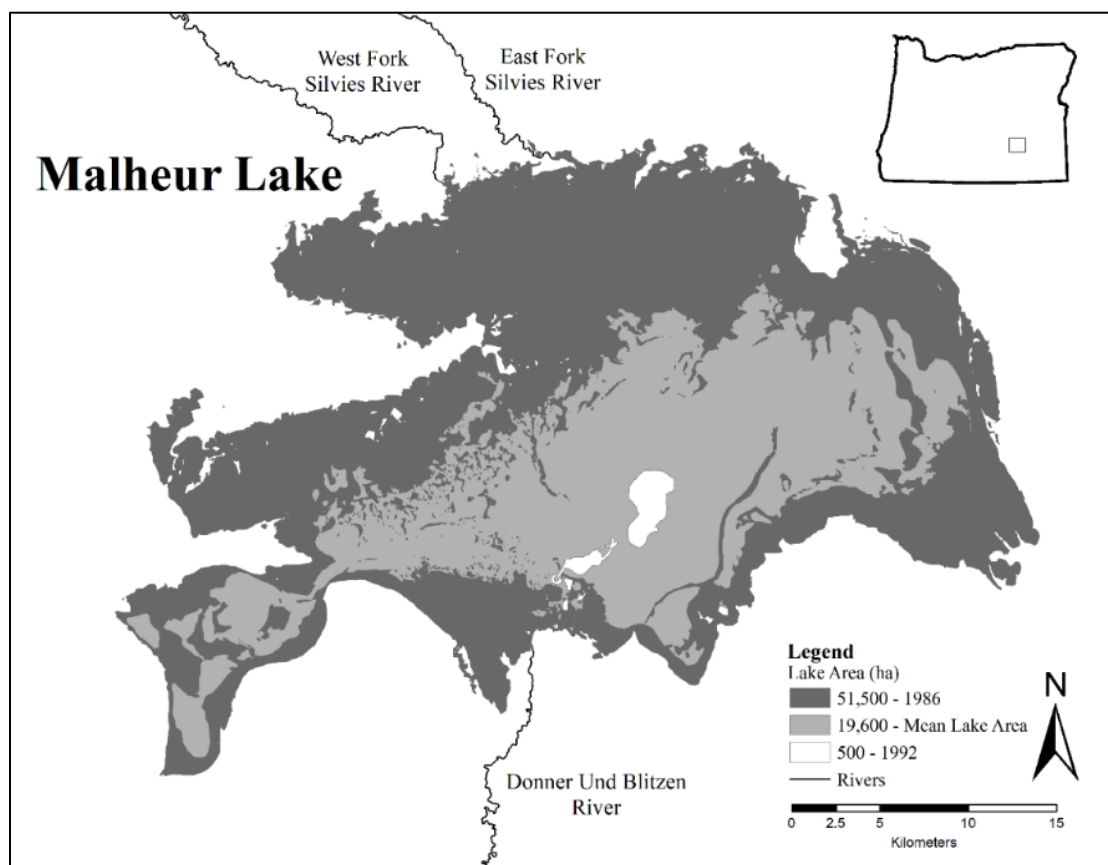


Figure 3.1. Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The dark gray region depicts the maximum lake area extent in 1986 ( $\approx 51,500 \text{ ha}$ ), the gray region depicts the average fall lake area ( $\approx 19,600 \text{ ha}$ ), and the light gray region depicts the lowest lake area extent in 1992 ( $\approx 550 \text{ ha}$ ).

### **Model Description: CarpMOD1.5**

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, stochastic model, executed on an annual time-step, and ran for 100 years. Five governing equations are used to simulate carp abundance, age structure, and length and weight in the model (Table 3.1 & 3.2). Juvenile carp recruit into the population after completing their first year of life (age 1), where recruitment is a density-dependent relationship between spawning adults and the number of juvenile recruits (age 0; Ricker, 1954; Koehn et al., 2000; Brown & Walker, 2004). 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+: kg/ha), whereby smaller carp experience greater mortality (Charnov et al., 2013; Bajer et al., 2015). Due to the prevalence of avian predation in Malheur Lake an additional mortality function is necessary to account for the annual consumption rates of small carp (< age 4) by avian piscivores (Wiens & Scott, 1975; Roby et al., 2003). Carp that survive, increase in length each year based on a Von Bertalanffy Growth Model (VBGM) and weight is calculated from an empirical length-weight relationship (Von Bertalanffy, 1938; Schneider et al., 2000; Jackson et al., 2008; Table 3.2). We built stochasticity into the recruitment equation (CarpMOD1.5) by specifying the model to randomly choose a parameter value for the Ricker Recruitment equation from a log-normal distribution each year of the model run. Adding demographic stochasticity to the recruitment section of the model likely allows more realism, since recruitment; Lee et al., 2011) is likely to vary among years due to a variety of factors that are unaccounted for in our model (e.g., water temperature, food availability, etc.; Edelstein-Keshet, 1988).

To simulate the affect that lake fluctuations will have on the carp population via density-dependent interactions, the carp population is tracked both as a total population (i.e. sum of

individuals in each age class) and also by density metrics (i.e. number of carp per hectare, number of mature carp per hectare, etc.). This model assumes that the carp are uniformly distributed throughout the lake, thus enabling us to ascribe a uniform mortality, recruitment, and adult reduction across the entire lake each year. Therefore, in years in which the lake area increases, the total carp population will initially be the same, however the density metrics will be decreased due to the same amount of carp evenly spread over a greater area.

For each model run there were two distinct phases: 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 of 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 ensure that modeled population did not go extinct due to chance fluctuations and that model outputs reflected the effects that environmental fluctuations and management scenarios had on an established carp population. The second scenario 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 years model run).

<sup>5</sup>Table 0.1 Equations used in CarpMOD1.5 to simulate the population dynamics of carp in Malheur Lake (Appendix A)

Model component	Equation	Reference
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	$\rho_i = (1 + e^{(\ln(19)((L_{(A)}-LM50)/(LM50-LM95)))})^{-1}$	Brown & Walker, 2004
Ricker Recruitment	$R = \alpha * S * \exp(-\beta * S)$	Ricker, 1954; Brown & Walker, 2004
Annual Natural Mortality (< 250 mm)	$V_{(A)} = (1 - e^{-0.06(\frac{L_{(A)}}{L_{\infty}})^{-1.5}} + 10^{-4} \cdot D)$	Charnov et al., 2013; Bajer et al., 2015
Annual Natural Mortality (> 250 mm)	$V_{(A)} = (1 - e^{-0.06(\frac{L_{(A)}}{L_{\infty}})^{-1.5}} + 10^{-4} \cdot D) \cdot (1 - AR)$	Charnov et al., 2013; Bajer et al., 2015
Adult Reduction Rate	$AR_T = \left(\frac{LA_F}{LA_A}\right) F_{eff}$	Constructed for this model

Table 0.2 Values for the CarpMOD1.5 parameters.

Parameters <sup>67</sup>	Symbol (Units)	Function	Value	S.D.	Description
Alpha Coefficient <sup>5</sup>	$a$ (x $10^{-5}$ )	W-L	4.531	0.0395	constant estimated by linear relationship
Beta Coefficient <sup>5</sup>	$b$	W-L	2.869	0.015	constant estimated by linear relationship
Theo Len. at Age 0 <sup>5</sup>	$t_0$ (mm)	VBGM	-0.548	0.250	theoretical length of carp at age zero
Growth Coefficient <sup>5</sup>	$K$ (years <sup>-1</sup> )	VBGM	0.133	0.020	rate at which theoretical maximum length is achieved
Theo Max Len. <sup>5</sup>	$L_{\infty}$ (mm)	VBGM	818.028	41.393	theoretical maximum length of carp
Alpha Coefficient <sup>6</sup>	$\alpha$	Recruitment	20.083	16.124	density-independent recruitment coefficient
Beta Coefficient <sup>6</sup>	$\beta$	Recruitment	0.0162	0.004	density-dependent recruitment coefficient
Len. of Maturity 50 <sup>6</sup>	LM50 (mm)	Maturity	309.667	31.754	length at which 50% of carp reach maturity
Len. of Maturity 95 <sup>6</sup>	LM95 (mm)	Maturity	364.667	47.343	length at which 95% of carp reach maturity
Lake Area Fished	$LA_F$ (ha)	AR	5000	-	Lake area fished annually
Lake Area Actual	$LA_A$ (ha)	AR	-	-	Lake area for a given year
Fishing Efficiency	$F_{eff}$	AR	0.95	-	Efficiency of fishing the given lake area ( $LA_A$ )

## Modeling Lake Area

Periodic observations of lake area have been collected at Malheur Lake by the MNWR refuge staff since 1938, however much of this data is qualitative and there are large gaps in observations (Duebbert, 1969). We reconstructed lake area for the 80 year period from 1938 to

<sup>5</sup> Table 3.1 Equations used in CarpMOD1.5 to simulate carp population dynamics. The Von Bertalanffy's growth model (VBGM) equation consists of  $L_{(A)}$  which is the length (mm) of carp at age (year),  $L_{\infty}$  is theoretical maximum length,  $k$  is the growth coefficient, and  $t_0$  is the theoretical length of 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, and  $L$  which is the length (Schneider et al., 2000). The Probability of Maturity equation consists of  $\rho_i$  which is the probability of maturity,  $L_{(A)}$  is the length at age,  $LM50$  which is the length at 50% maturity, and  $LM95$  which is the length at 95% maturity (Brown et al., 2003). The Ricker Recruitment Model consists of  $R$  which is the total annual recruits per hectare (total recruits = recruits per hectare x lake area),  $S$  is the numbers of mature individuals per hectare (number of mature carp per hectare = total mature carp population / lake area),  $\alpha$  is the density-independent coefficient,  $\beta$  is the density-dependent coefficient (Ricker, 1954). The Annual Natural Mortality equations consists of  $V_{(A)}$  which is the annual mortality at age  $A$  of carp,  $L_{(A)}$  is the average length of carp at age  $A$ ,  $L_{\infty}$  is the asymptotic average length of the carp population,  $D$  is the density of age 1 + carp (kg/ha; density of age 1 + carp = total age 1 + carp / lake area), and  $AR$  is the adult reduction rate (Charnov et al., 2013; Bajer et al., 2015; Pearson et al., 2019). The  $AR_T$  is proportional to the lake area, and the  $LA_F$  is the lake area fished,  $LA_A$  is the lake area actual, and  $F_{eff}$  is the fishing efficiency.

<sup>6</sup> Derived via data collected from Malheur Lake

<sup>7</sup> Brown & Walker 2004; Brown & Gilligan 2014



2018 by building a basic hydrologic model that predicts autumn lake area (October 1<sup>st</sup>) using a collection of satellite images and environmental variables (1978-2018). Lake areas were quantified for October 1<sup>st</sup> 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).

Using Landsat Satellite Imagery ([landsatlook.usgs.gov](https://landsatlook.usgs.gov); Landsat 1-8 satellites; 1972-2017) collected nearest to October 1<sup>st</sup>, on days with less than 20% cloud cover, a continuous 45 year dataset of lake area was assembled for Malheur Lake. To quantify lake area, a spectral analysis was conducted on each Landsat image using the near infra-red band (NIR Band 1; 700-2500 nm). A spectral analysis classification categorized individual images into three distinct spectral regions that correlated to: 1) open water, 2) wetlands, and 3) land, with a manual reclassification differentiating the wetland pixels into land or water (McFeeters, 1996; Huang et al., 2003; Lillesand, et al., 2014). Once all pixels were categorized, the water pixels were quantified using ArcGIS (Calculate Geometry; ArcMap Version 10.5; Environmental Systems Research Institute, Redlands, CA USA) to determine the lake area (ha) for each image.

To construct the basic hydrologic model, we analyzed a suite of variables (discharge, precipitation, temperature; Table 3.3). The precipitation variables analyzed were snow depth (cm) and snow water equivalent (SWE: cm), collected at two SNOTEL sites, one in the Steens Mountains (Fish Creek: 2335m) and one in the Blue Mountains (Starr Ridge: 1600m). The discharge variables were total discharge (cms; water year) and 50% total discharge (Julian date) on the Donner und Blitzen River (USGS – 10396000: Donner und Blitzen River near Frenchglen, OR). The temperature variables were total annual water year (1 Oct. – 30 Sept.) air temperature (C; degree days) and summer air temperature (1 June – 30 Sept.; Burns Municipal Airport – OR Automated Surface Observing System (ASOS)). Additional

environmental variables were considered (Silvies River discharge, evapotranspiration, soil moisture content, etc.), however they were ultimately left out due to a lack of continuous data for the time period modeled.

Table 0.3. Parameters used to predict Malheur Lake area fluctuations.

Parameters	Units	Model Input Name	Length of Dataset	Source <sup>8</sup>
Fall Lake Area	ha	FA_LA	1972 - Present	LandSat
Fall Lake Area (Previous Year)	ha	FA_LA_M1	1972 - Present	LandSat
Fish Creek Total Snow Accumulation	cm	FC_CM_MAX	1980 - Present	SNOTEL/NRCS
Fish Creek SWE	cm	FC_SWE_MAX	1980 - Present	SNOTEL/NRCS
Star Ridge Total Snow Accumulation	cm	SR_CM_MAX	1981 - Present	SNOTEL/NRCS
Star Ridge SWE	cm	SR_SWE_MAX	1981 - Present	SNOTEL/NRCS
Degree Day Temps (Water Year)	C	WY_TEMP_C	1974 - Present	Oregon ASOS/AWOS
Degree Day Temps (Summer Months)	C	JJAS_TEMP_C	1974 - Present	Oregon ASOS/AWOS
Blitzen River Discharge	cms	WY_BLITZ_CMS	1923 - Present	USGS
Blitzen River 50% Discharge	day	WY_BLITZ_DAY_50_DIS	1923 - Present	USGS

We used R-Computing Software (The R Foundation, Vienna, Austria) to run a multiple linear regression to determine the best-fit model for predicting annual lake areas. Explanatory variables were first tested for multicollinearity via the quantification of variance inflation factors (VIF), and variables with a VIF value >10 were removed (Belsley et al., 1980). We used a stepwise model selection procedure to construct the most parsimonious model (Queen et al., 2002).

## Carp Removal

To explore how carp removal efforts are influenced by lake 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 non-target species (Colvin et al., 2012; Pearson et al., 2019). To simulate the removal of adult carp, we assumed that the adult harvest rate (AR; the proportion of the adult population that is removed)

<sup>8</sup>LandSat: <https://landsatlook.usgs.gov/viewer.html>; SNOTEL/NRCS: <https://www.nrcs.usda.gov/wps/portal/nrcs/main/or/snow/products/>; Oregon ASOS: [https://www.faa.gov/air\\_traffic/weather/asos/?state=OR](https://www.faa.gov/air_traffic/weather/asos/?state=OR); USGS: <https://waterdata.usgs.gov/or/nwis/current/?type=flow>

was proportional to the size of the lake. This relationship assumes that harvest pressure (e.g. the area of the lake that nets are set) remains the same across different lake areas, which results in lower removal rates when the lake is large (parameter values in Table 3.2).

### **Carp Model Scenarios**

We used CarpMOD1.5 to simulate the historical carp population fluctuations using the reconstructed lake areas (1938-2018) and tested the effects of alternative carp removal strategies (no removal - NR; low water year removal - LWYR < 10,000 ha; all year removal - AYR) on the population dynamics. Specifically, we explored how successful removal strategies are at maintaining the carp biomass < 50 kg/ha (hypothesized threshold at which waterfowl productivity increases; Vilizzi et al., 2015). Each scenario was simulated 10,000 times, giving 10,000 separate estimates of carp biomass, of which a time series graph was constructed using the median model outputs for each year. Box-and-whisker plots were also constructed using the overall mean carp biomass (all years combined) and proportion of years that the carp biomass fell below the threshold (< 50 kg/ha).

We then conducted a suite of simulations to explore how fluctuations in lake area affect carp populations and removal efforts. To do this we developed a set of deterministic lake area fluctuations, whereby we adjusted the duration and magnitude of high and low lake areas (Figure 3.2). These scenarios were meant to simulate potential increased drought conditions predicted to occur in the Great Basin (Dalton et al., 2018; Snyder et al., 2019), which are likely to reduce the number of years of larger lake areas, as well as decrease the size of the lake during years of both high and low lake areas (i.e., lower highs and lower lows). Three high and low lake area duration scenarios were selected that represent a progression towards fewer years in which the lake is high: 1) 6 years of high lake area and 6 years of low lake area (6x6), 2) 4 high and 8 low (4x8), and 3) 2 high and 10 low (2x10). For each duration scenario, we then adjusted

the magnitude of the lake area during high and low years: 1) high lake area (HLA - Max: 30,000 Min: 12,500, 2) medium lake area (MLA - Max: 25,000 Min: 7,500), and 3) low lake area (LLA - Max: 20,000 Min: 2,500). This resulted in a total of nine deterministic lake area fluctuations (Figure 3.2). For each of these lake area scenarios we simulated the total carp population under each removal scenario: 1) NR, 2) LWYR, and 3) AYR.

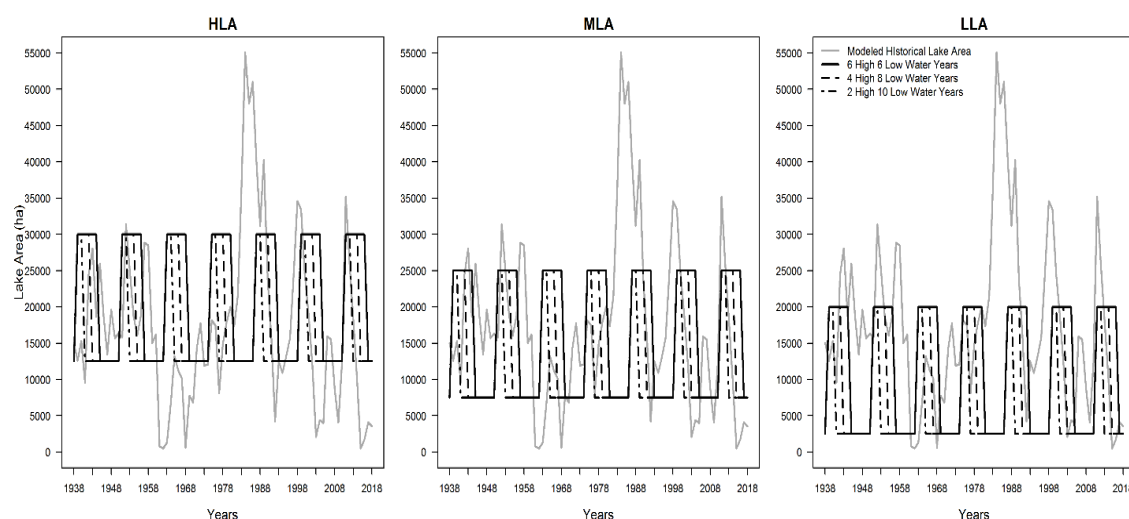


Figure 3.2. Carp population dynamics were simulated under nine deterministic lake area scenarios, which represent different combinations of high and low lake areas, including three duration scenarios: 1) 6 high and 6 low (6x6; solid black line), 2) 4 high and 8 low (4x8; dashed black line), and 3) 2 high and 10 low (2x10; dashed and dotted black line) and three lake area scenarios: 1) high lake area (HLA - Max: 30,000 Min: 12,500, 2) medium lake area (MLA - Max: 25,000 Min: 7,500), and 3) low lake area (LLA - Max: 20,000 Min: 2,500). Deterministic lake simulations are overlaid on modeled lake area for 1938-2018.

In addition to these deterministic simulations, we also simulated future carp biomass under different stochastic lake area simulations using our lake area model. 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 (multiple linear regression model). We implemented three future lake area scenarios: 1) base (no change), 2) base -12.5%, and 3) base -25%. Therefore, the future base scenario used the lake area model to output a new lake area annually, and this was repeated yearly for the

entirety of the scenario simulation (years 51 - 130). The base -12.5% and base -25% scenarios simply took the annual lake area output from the multiple linear regression model and subtracted 12.5% or 25% respectively (predicted  $\approx 30\%$  decrease in SWE by mid-century in Pacific Northwest; Mote et al., 2014; Naz et al., 2016). For all model scenarios we ran the model 10,000 times, which resulted in 10,000 separate estimates of carp biomass. Results were displayed using box-and-whisker plots that show the range of responses across the 10,000 model runs.

## **Results**

### **Modeling Lake Area**

The hydrologic model closely matched the observed lake area dynamics of Malheur Lake during the years when empirical lake area estimates were available ( $R^2 = 0.948$ ; Adjusted  $R^2 = 0.943$ ;  $F(3,32) = 193.9$ ;  $p < 2.2e^{-16}$ ). Lake area was best predicted by: 1) previous year's lake area (ha; FA\_LA\_M1), 2) discharge (cms; water year; WY\_BLITZ\_CMS) from the Blitzen River, and 3) date of 50% total discharge (Julian date; WY\_BLITZ\_DAY\_50\_DIS) from the Blitzen River (described further in Appendix C).

### **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. The carp biomass generally peaked in years following large drops in lake area due to the confinement of the carp population. In contrast, years in which the lake area is increasing, the carp biomass 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 (NR) produced a median carp biomass of  $573 \pm 367$  kg/ha (median  $\pm$  standard deviation), which fell below the 50 kg/ha threshold in  $17 \pm 20\%$  of simulated years

(Figure 3.3 & 3.4). Outputs from the low water year removal (LWYR) scenario resulted in a median carp biomass of  $432 \pm 277$  kg/ha with the carp biomass falling below the designated threshold in  $37 \pm 19\%$  of simulated years. Outputs from the all year removal (AYR) scenarios resulted in a median carp biomass of  $216 \pm 153$  kg/ha with the carp biomass falling below the desired biomass threshold in  $48 \pm 22\%$  of simulated years.

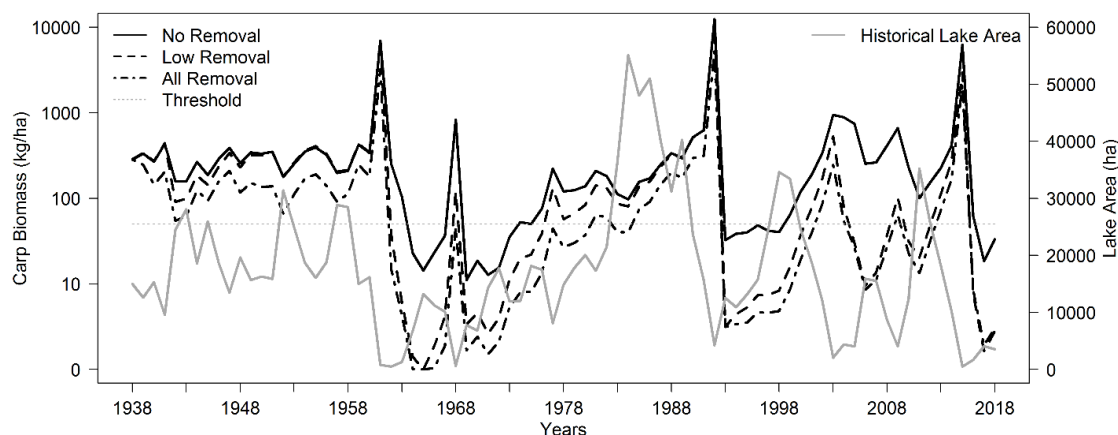


Figure 3.3. Simulated median carp biomass (kg/ha) of 10,000 model runs per removal scenario (NR, LWYR, AYR), using historical lake levels (1938-2018). Solid black line is the carp biomass under the no removal (NR) scenarios, black dashed line is the carp biomass under the low water year removal (LWYR) scenario (<10,000 ha), and black dotted line is the carp biomass under the all year removal (AYR) scenario.

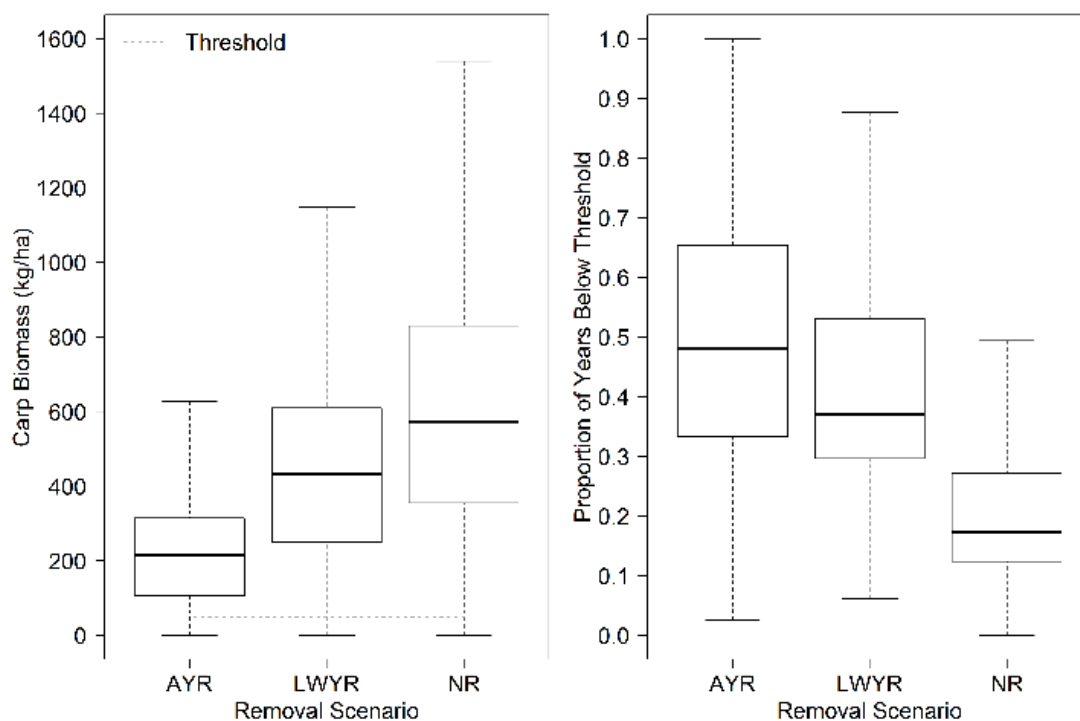


Figure 3.4. Left: Median carp biomass (kg/ha) outputs using the historical lake area (1938-2018) under the three individual removal scenarios (NR, LWYR, and AYR). The dashed horizontal line indicates a target threshold of 50 kg/ha). Right: Median proportion of years for which the carp biomass fell below the designated threshold under each removal scenario using historical lake areas. Box-and-whisker plots demonstrating the sensitivity of modeled outputs to uncertainty in model parameter values. The bold black lines within each box are the median outputs, outer edges of box are 0.25 and 0.75 quantiles, and outer whiskers are 0.05 and 0.95 quantiles.

Heuristic lake area simulations demonstrated that shifts in the magnitude and duration of high and low lake areas can have a large influence on modeled carp biomass. Simulations with a greater duration of high-water years (i.e. 6 low x 6 high years; Figure 3.2) led to greater mean, maximum, and minimum carp biomass under all carp removal scenarios (NR, LWYR, AYR; Figure 3.5 & Table 3.4), whereas decreased duration of high-water years (i.e. 2x10) had the opposite result (i.e. lower carp biomasses). The greatest peaks (maximum) in carp biomass coincided with the low lake areas (LLA) and increased duration of high-water years (i.e. 6x6). Removal measures targeting adult carp were more effective in the simulations with lower lake area (LLA), and a greater proportion of low water years (i.e., 2x10). Lastly, all simulations conducted with short durations of high lake areas (i.e. 2x10) had a minimum median carp

biomass below 50 kg/ha, meaning that the median carp biomass fell below the desired threshold at least once during these simulations.

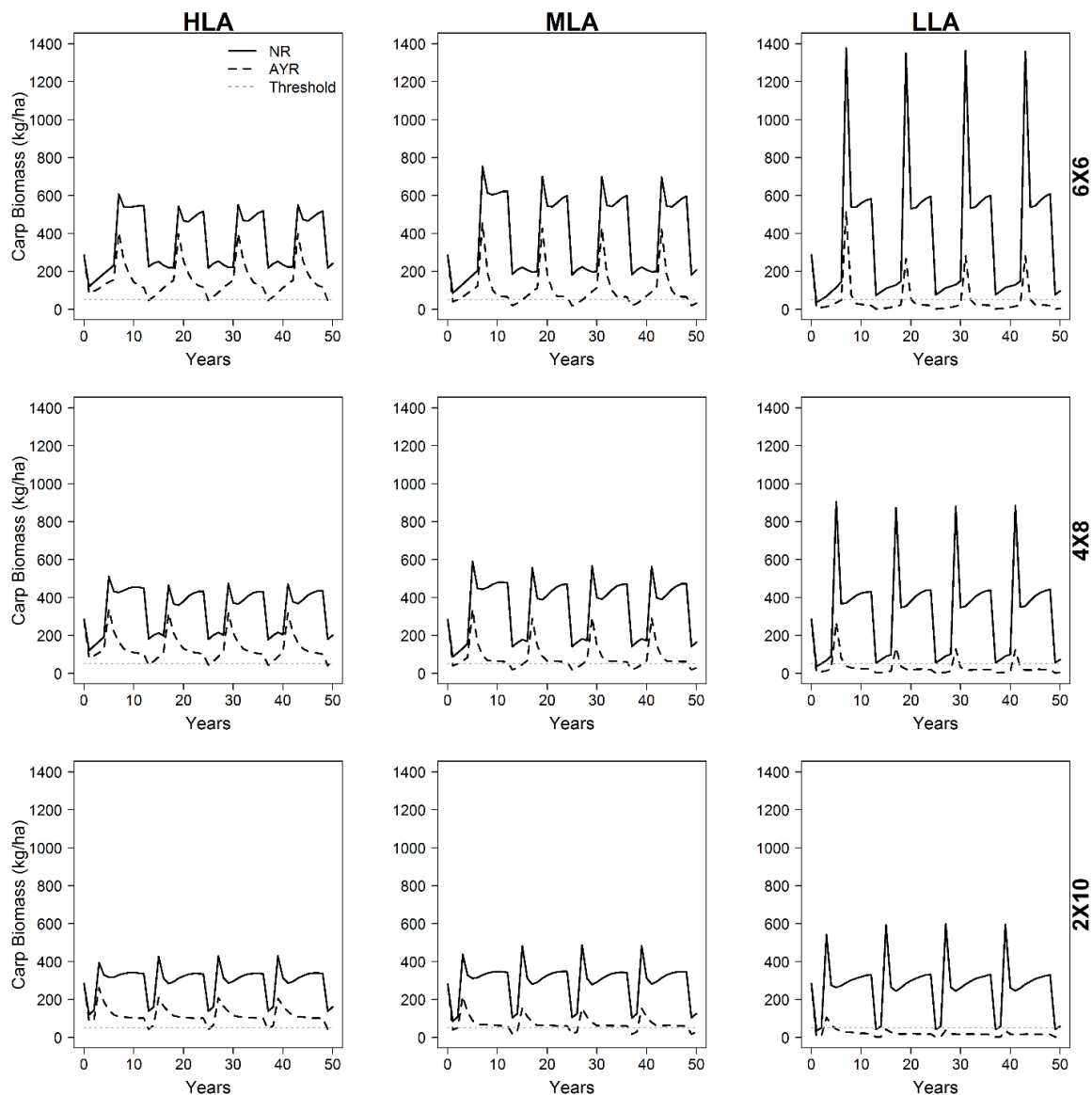


Figure 3.5. Median modeled carp biomass (kg/ha) outputs for the 10,000 model runs for each lake area scenario. The solid black line represents no removal (NR) and the dashed black line represents all year removal (AYR) of carp. The graphical columns represent the three hydrologic lake area categories (HLA – high lake area, MLA – medium lake area, LLA – low lake area), while the graphical rows represent three duration scenarios: 1) 6 high and 6 low (6x6), 2) 4 high and 8 low (4x8), and 3) 2 high and 10 low (2x10; Figure 3.2; see Methods). The low water year removal (LWYR) scenario was left out because it exhibited a similar response with slightly higher peaks due to removal only during low years (describe in more detail in discussion).



### **Future Hydrologic Variability: Fluctuations and Carp Removal Scenarios**

Future lake area fluctuation model results (described in detail in Appendix C) demonstrated that the carp biomass decreased slightly with decreasing lake area (NR – Base:  $545 \pm 367$ , Base -12.5%:  $502 \pm 360$ , Base -25%:  $453 \pm 346$  kg/ha; median  $\pm$  standard deviation), and the proportion of years in which the carp naturally fell below the desired biomass threshold increased with decreasing lake area (NR – Base:  $16 \pm 20\%$ , Base -12.5%:  $22 \pm 21\%$ , Base -25%:  $23 \pm 20\%$ ; Figure 3.6). Carp removal strategies targeting adult carp were also more successful with decreasing lake areas (LWYR – Base:  $197 \pm 170$ , Base -12.5%:  $117 \pm 114$ , Base -25%:  $78 \pm 84$  and AYR – Base:  $120 \pm 95$ , Base -12.5%:  $82 \pm 80$ , Base -25%:  $61 \pm 70$  kg/ha), and years in which the carp biomass was able to be suppressed below the desired threshold increased with decreasing lake area (LWYR – Base:  $48 \pm 23\%$ , Base -12.5%:  $65 \pm 21\%$ , Base -25%:  $75 \pm 20\%$  and AYR – Base:  $54 \pm 25\%$ , Base -12.5%:  $70 \pm 21\%$ , Base -25%:  $78 \pm 20\%$ ).

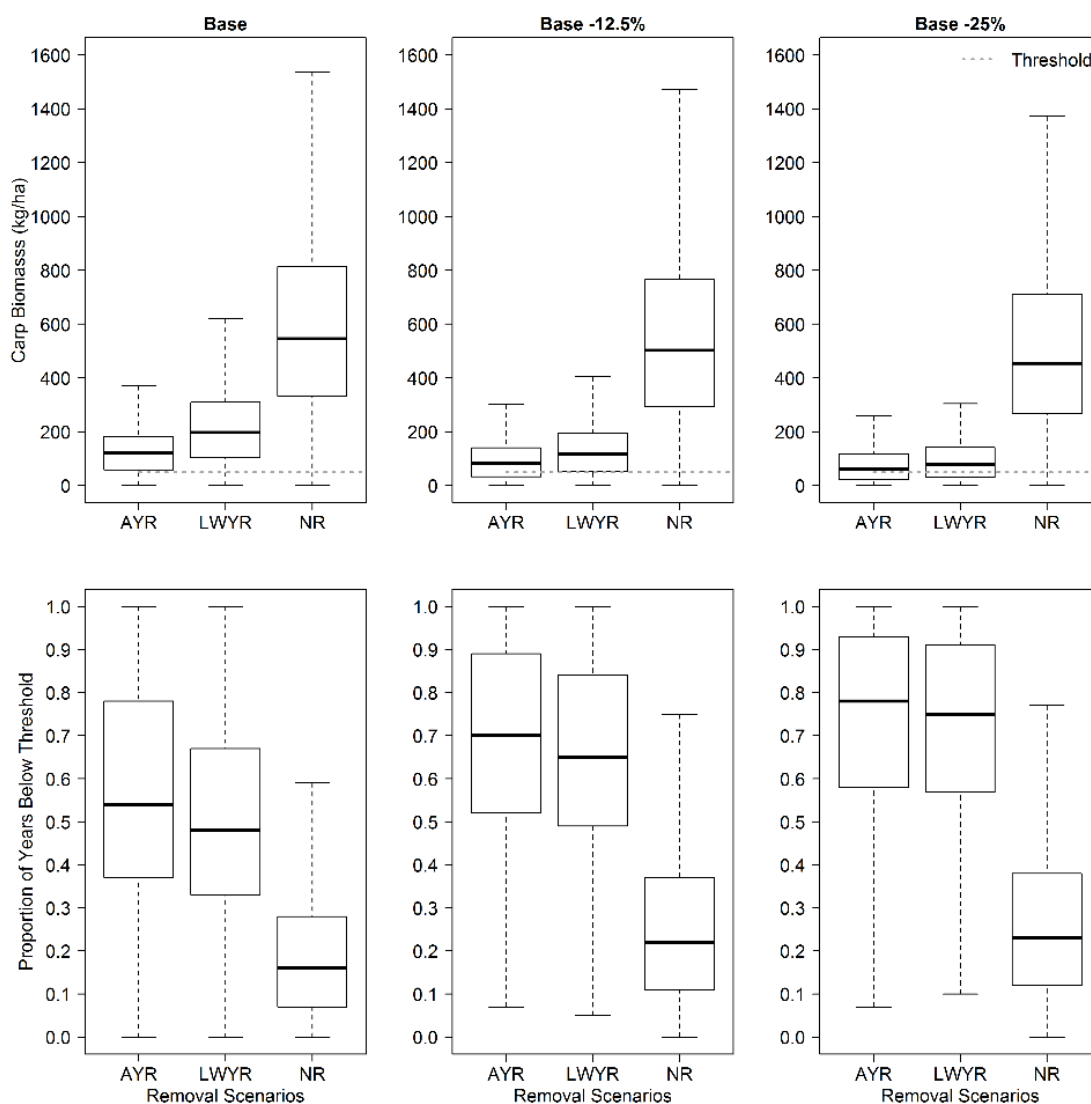


Figure 3.6. Modeled carp population outputs with simulated declines in lake area of Malheur Lake. The graphs in the left column were simulated using the base (contemporary lake areas) scenario, the graphs in the center column are the base hydrologic scenario with a 12.5% reduction in lake area, and the graphs on the right are a 25% reduction. The top row of graphs displays the mean carp biomass (kg/ha) under the three carp reduction scenarios (NR – No Removal, LWYR – Low Water Year Removal, AYR – All Years Removal). The bottom row of graphs displays the average proportion of years in which carp biomass falls below the 50 kg/ha threshold. Box-and-whisker plots display sensitivity in modeled values to uncertainty in both hydrologic fluctuations and uncertainty in model parameter values. 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**

We simulated carp population dynamics under a suite of hydrological regimes and these simulations suggest that lake area fluctuation strongly influences carp biomass 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 suggest that systems like Malheur Lake will become drier and thus non-native carp populations will likely decline and the efficacy of control efforts will increase. Although this may be deemed a desirable outcome, prolonged dry conditions are also likely to diminish the likelihood of achieving desired ecological conditions (e.g., clear water, abundant submergent macrophytes, water birds, etc.) in Malheur Lake and other carp dominated waterbodies (Nielsen & Brock, 2009).

The model dynamics show the potential for significant peaks and troughs in carp biomass brought on by lake fluctuations. During low water years (i.e. low lake area), the carp are confined to a small area creating a peak in carp biomass and causing decreased recruitment and increased natural mortality (Maiztegui et al., 2019). During high water years the carp population spreads out into the newly inundated area creating troughs in carp biomass, in which the carp population is able to grow under less restricted 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 growths and declines. The peaks in carp biomass are further exacerbated in years following prolonged high water years (large lake area) because the carp population has more time to recover from low water events and grow under density independent conditions.

Fish species (e.g. Common carp) that survive and grow best in highly variable environments are referred to as periodic fish species (large, highly fecund, 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, 1992). Periodic fish species 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 (i.e. periodic fish species) 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, non-native periodic fish species (e.g. carp, striped bass (*Morone saxatilis*), American Shad (*Alosa sapidissima*)) are extremely difficult to control, and even more so 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. Specifically, we found that the targeting of adult carp during low water years (LWYR) can result in an overall lower carp biomass with more years below the threshold whereby ecological recovery is predicted (50 kg/ha). 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 (proportion of years below  $\approx 37\%$ ), relative to the no removal (NR) scenario (proportion of years below  $\approx 17\%$ ; Figure 3.3 & 3.4). However, removing carp during all years (AWY; 80 years) only showed a moderate increase in years below the ecological threshold (proportion of years below  $\approx 48\%$ ), despite the addition of 61 more years of adult reduction efforts, thus 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, extent of droughts), with decreasing snow water equivalent throughout the 21<sup>st</sup> century (Trenberth & Fasullo, 2013; Lute et al., 2015; Crausbay et al., 2017; Black et al., 2018). 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 to control them. For instance, results suggest that fewer high lake areas (period) will decrease the overall carp biomass (Figure 3.5). These climatic changes will also increase the ability to control the carp population via adult removals in the future (i.e. lower lake area increases removal efficiencies). However, while the deterministic and future model scenarios predicted a decrease in the overall carp biomass, these simulations also predict increased peaks in carp biomass during low water years. Therefore, future research may be needed to examine how these greater peaks in carp biomass may adversely affect the invaded aquatic ecosystems, potentially exacerbating the carp population's already deleterious impacts.

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 (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 semi-arid regions (Moss et al., 2011; Costa et al., 2016; 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 rely on semi-annual 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 which promote phytoplankton growth (Carper & Bachmann, 1984; James et al., 2004; Scheffer et al., 2007). Therefore, there are likely to be diminished returns from non-native species control in the future as the climate becomes more arid.

Results of this modeling work highlight the challenge of active removal efforts as a means of controlling non-native fishes, such as carp. A recent review of control measures for non-native fishes documented a series of notable successes, but these were overwhelmingly reported from smaller and more isolated systems (Rytwinski et al., 2018). 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 invasive species often emphasizes early detection and control (Reaser et al., 2019), but many invaders such as carp are well-established across broad extents and extremely difficult to control (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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#### **Chapter 4: A Spatially Explicit Sediment Resuspension Model to Evaluate Physical Controls on Clear and Turbid States in a Large-Shallow Lake Ecosystem**

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## **Abstract**

Shallow lakes exist in two alternative stable states: clear or turbid, and the shift from a clear to a turbid state can be induced by several factors (i.e. climatic, loading of nutrients, water level fluctuation, bioturbation), with these same factors increasing a system's resilience to a shift back to the clear state via positive feedback mechanisms. The introduction of the non-native Common Carp (*Cyprinus carpio*) has been hypothesized as responsible for the degradation of the aquatic ecosystem in Malheur Lake, a shallow lake-wetland ecosystem in southeast Oregon, USA (Pearson et al. 2019). Here, we examined how wind resuspension may also be contributing to the overall turbid environment in this system and potentially acting to prevent a shift back to a clear state. We constructed a wind resuspension model to simulate how variations in environmental and morphological drivers may affect the overall suspended sediment concentrations (SSC; mg/L) in Malheur Lake. Due to the unique nature of Malheur Lake (i.e. long wind fetches, shallow depths, and sediment characteristics), we constructed two distinct erosion-deposition modules that worked additively to simulate the physical action of wind resuspension on both a heavier and lighter sediment fractions. The wind resuspension model was ultimately used to determine the efficacy of alternative restoration actions in the form of wave reduction barriers. Simulations demonstrated that fluctuations in lake area cause large disparities in the mean overall SSC in Malheur Lake, with the greatest SSC exhibited at the lowest modeled lake area (1247.75 m) and the lowest SSC at the highest lake area (1248.75 m). Furthermore, the models simulating the efficacy of wave reduction barriers demonstrated a large reduction in the mean overall SSC, thus suggesting that wave reduction barriers may be useful in assisting large scale restoration efforts in Malheur Lake. Ultimately, this project furthered our understanding of the relationships between environmental factors (wind speed and wind direction), lake morphometry (lake area, water depth, and wind fetch), alternative restoration actions (wave reduction barriers), and the overall SSC in the surrounding aquatic ecosystem of Malheur Lake.

## **Introduction**

Shallow lakes exist in two alternative states: clear or turbid, with the clear state characterized by an abundance of aquatic macrophytes, diverse aquatic biota, low water column nutrients and phytoplankton biomass, whereas the turbid state is characterized by the opposite (Scheffer et al. 1993; Scheffer & Jeppesen, 2007; Scheffer & van Nes, 2007). A shift from a clear to a turbid state can be induced by several factors (i.e. climatic, loading of nutrients, water level fluctuation, bioturbation), and these same factors can create resistance to state change (Hargeby et al., 2004). One mechanism that creates resistance to a change from the turbid to clear state is wind-driven sediment resuspension (Van Duin et al., 2001; James et al., 2004; Scheffer & van Nes, 2007).

As wind travels across a lake's surface, it creates energy that generates circular waves extending to the sediment, which results in a shearing action that suspends sediment into the water column and creates a turbid state (CERC, 1984; Carper & Bachmann, 1984). Large shallow lakes are especially susceptible to wind suspension due to their large surface area, long wind fetches, and shallow depths (Håkanson, 1982). As the wind fetch lengthens, wave energy increases (wave height and wave period), thus resulting in an increased shear stress along the lake bottom (CERC, 1984; Scheffer & van Nes, 2007). These factors combine to create a turbid environment with concomitant reductions in aquatic macrophytes, zooplankton, and piscivorous fish (Van Duin et al., 2001; Scheffer, 2001; James et al., 2004).

Wind-driven sediment resuspension also adds to the overall turbidity of shallow lakes through the delivery of phosphorous into the water column (Søndergaard et al., 1992; Søndergaard et al., 2003; Qin et al., 2006). Phosphorous bound to sediment particles accumulates in the sediment of shallow lakes as vegetation decays and is released into the water column



(dissolved/particulate) during wind resuspension events due to differences in concentrations (Wang et al., 2015). Bioavailable phosphorous delivered into the water column via wind resuspension can subsequently be used by phytoplankton, thus increasing the biomass of phytoplankton, which further reduces the clarity of the water column (Tang et al., 2019). In some lakes, sediment resuspension adds excessive phosphorous to the water column, thus enabling phytoplankton species that can fix atmospheric nitrogen (e.g. cyanobacteria) to outcompete other phytoplankton species (Scheffer et al., 1997; Ibelings et al., 2007; Bormans et al., 2016).

The mechanisms driving both forms of turbidity are related to the resuspension of sediment; therefore, decreasing the physical act of sediment resuspension via wind will likely decrease turbidity and increase water clarity (i.e. increase the penetration depth of photosynthetic active radiation (PAR); Bormans et al., 2016). However, the effects of wind energy on the physical characteristics of a lake are complex due to the interactions of water depth, wind speed, and wind fetch (Scheffer & van Nes, 2007). Therefore, to better understand these complexities, researchers use mechanistic models to evaluate control efforts prior to implementation (Howard-Williams, 1985; Prescott & Tsanis, 1997; Chow-Fraser, 1998; Penning et al., 2013).

Considering that the main mechanisms driving both forms of turbidity are related to the resuspension of sediment, then decreasing the physical act of sediment resuspension will likely decrease turbidity and increase water clarity (i.e. increase the penetration depth of PAR; Bormans et al., 2016). However, the effects of wind energy on the physical characteristics of a lake are complex, and therefore restoration alternatives meant to limit sediment re-suspension may have varying success depending on individual lake morphometry (Scheffer & van Nes, 2007; Penning et al., 2013). Therefore, to better understand these complexities, mechanistic models have been applied to evaluate alternative restoration actions prior to implementation

(Howard-Williams, 1985; Prescott & Tsanis, 1997; Chow-Fraser, 1998). These mechanistic models can also serve to link scientists, managers, and stakeholders, throughout the modeling process, which in turn maximizes the effectiveness of any resulting scientific insights (Cash et al., 2003).

In this study, we developed a one-dimensional (vertically averaged) wind resuspension model to simulate variations in suspended sediment concentrations (SSC) in response to environmental and morphological drivers including wind speed, wind fetch, and water depth (Chao et al., 2008; Liu et al., 2019). The wind resuspension model was applied to Malheur Lake, a large, shallow, endorheic wetland-lake system in the Great Basin region of southeastern Oregon USA. The wind resuspension model was used to simulate both the current aquatic environment (corroborated by *in situ* monitoring) as well as the efficacy of alternative restoration actions in the form of wave reduction barriers aimed at reducing the SSC and subsequently increasing the overall light availability within the water column in Malheur Lake. Wave reduction barriers were selected as an alternative restoration action due to their ability to reduce the overall turbidity via decreasing wind fetch and bottom shear stress (Penning et al., 2013). Due to the unique nature of Malheur Lake (i.e. long wind fetches, shallow depths, and sediment characteristics), we constructed two distinct erosion-deposition modules that worked additively to simulate the physical action of wind resuspension on both a heavier sediment fraction (i.e. slow to respond to wind events and quick to fall out of suspension) and a lighter sediment fraction (i.e. quick to respond to wind events and slow to fall out of suspension). Due to the potential for large annual lake fluctuations in Malheur Lake, simulations were conducted using a range of lake areas to determine how the efficacy of the wave reduction barriers may shift as the lake area fluctuates. Ultimately, this project furthered the understanding of the relationships between environmental factors (i.e. wind speed and wind direction), lake

morphometry (i.e. lake area, water depth, and wind fetch), alternative restoration actions (wave reduction barriers), and the overall SSC in the surrounding aquatic ecosystem.

## **Methods**

### **Study Area**

Malheur Lake is located in Southeastern Oregon (Lat: 43.3115 and Long: -118.7952) and is one of the largest freshwater marshes in North America, serving as an important migration and breeding area for fresh water wetland birds (Duebbert, 1969; Cornely, 1982; MNWR, 2012). Malheur Lake is located within the Malheur National Wildlife Refuge (MNWR) and is managed by the U.S. Fish and Wildlife Service (USFWS). Malheur Lake is a large (average  $\approx 19,600$  ha), shallow (average depth  $\approx 0.58$  m; max depth  $\approx 1.26$  m), polymictic, terminal lake (endorheic basin), that exhibits large annual lake fluctuations ( $\approx 51,500$  ha in 1986 to  $\approx 550$  ha in 1992; Hubbard, 1975; Miller, 2012; Figure 4.1). The lake is fed by two major freshwater inputs, the Silvies and Donner und Blitzen Rivers, which drain a total watershed of roughly  $7,770 \text{ km}^2$  (Miller, 2012; Williams et al., 2014). The mean annual temperature at Malheur Lake is  $7.94^\circ\text{C}$  with July being the warmest month (mean:  $26.39^\circ\text{C}$ ) and January as the coldest month (mean:  $-7.56^\circ\text{C}$ ; Williams et al., 2014), with ice forming and persisting on Malheur Lake throughout the winter months (December – February).

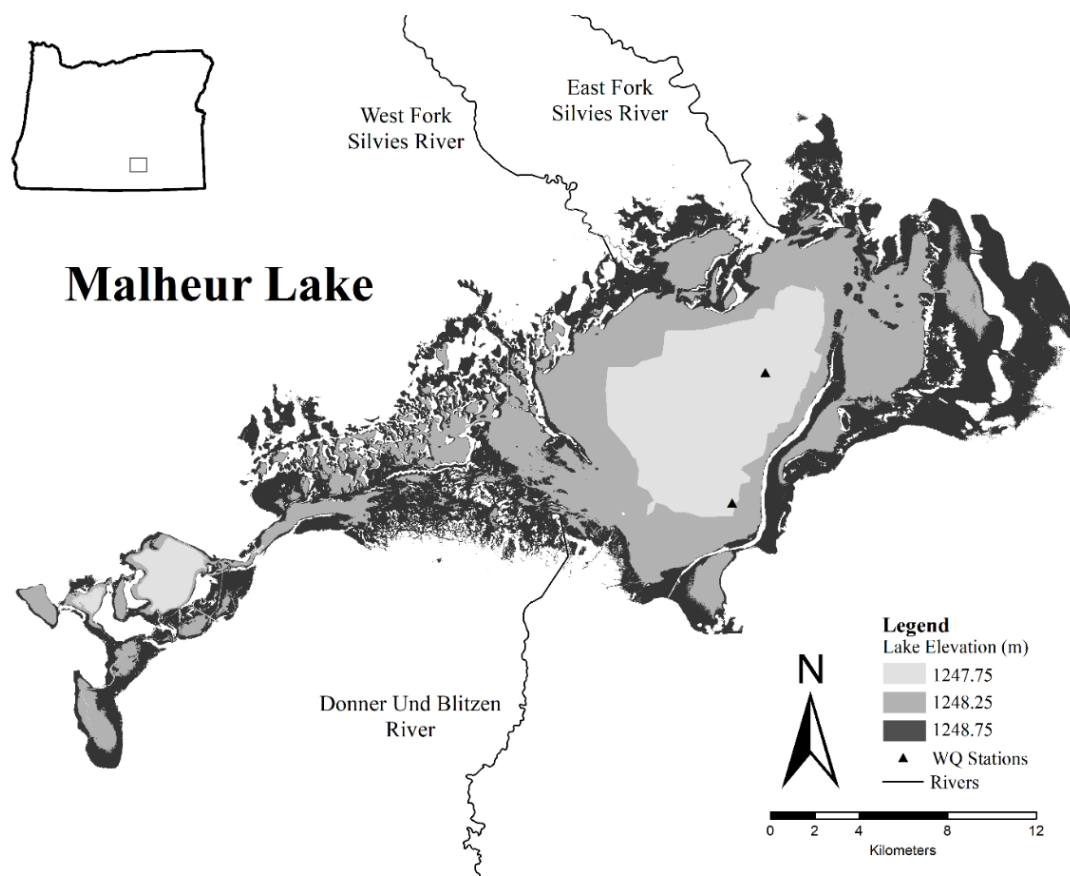


Figure 4.1. Map of Malheur Lake, located within the Malheur National Wildlife Refuge in Southeastern Oregon. The dark gray region depicts the lake area at 1248.75 m (3,663 ha), the medium gray region depicts the lake area at 1248.25 m (11,071 ha), and the light gray region depicts the lake area at 1247.75 m (19,952 ha; average fall lake area  $\approx$  19,600 ha).

### Data Collection

Water quality data was collected *in situ* at Malheur Lake for three years (2017-2019) to aid model construction, calibration, and validation. Water quality data was collected at two locations (NE Site - Lat: 43.334531 and Long: -118.759472; SE Site - Lat: 43.307208 and Long: -118.782142) in Malheur Lake, with continuous and bi-weekly point data collected (turbidity, conductivity, chlorophyll a) using sondes (YSI 6600 V2; YSI Inc.; Yellow Springs, Ohio, USA; Figure 4.1). We selected sampling sites to maximize wind fetch lengths from the predominant wind direction (230 degrees; NE Site  $\approx$  8.5 km and SE Site  $\approx$  4.0 km) and increased spatial distance between sites ( $\approx$  4.4 km), while also maintaining enough water depth to ensure instruments remained submerged throughout the study period.

### **Wind Resuspension Model - Assumptions**

The oscillating velocities of wind waves at the sediment-water interface generally exceed the mean currents in a shallow lake subject to strong wind forcing, and in these cases the contribution of the mean currents to the bottom shear stress is quite small in comparison to the wave-induced currents and can usually be ignored (Luettich et al., 1990; Chung, et al., 2009b; Li et al., 2017; Jalil et al., 2019). Furthermore, the assumption is often made when modeling SSC in a large and shallow lake that the primary mechanism driving SSC in the water column at a given location is localized resuspension and deposition, and that advection by mean currents and horizontal dispersion by turbulent eddies are small in comparison (Carper & Bachmann, 1984; Bachmann et al., 2000; Cózar et al., 2005; de Vicente et al., 2009; Li et al., 2017). To the extent that the assumption is valid, the evolution of SSC can be independently calculated at each location in the lake, by converting wind energy to wave energy based on the fetch, and then transmitting the wave energy through the local water column to the sediments where it is converted to shear stress. Resuspension and deposition are then calculated based on local sediment characteristics. In this simplification, therefore, the only influence the surrounding water body exerts on SSC at a point is the distance to the shoreline, measured into the direction of the wind (wind fetch). Horizontal advection and dispersion can be expected to have a smearing effect on horizontal gradients in SSC; however, our data collection indicated that turbidity in the lake is consistent over long distances and responds similarly to large-scale wind events at short (sub-daily to several days) time scales (Figure 4.2). We concluded, therefore, that large-scale horizontal gradients that would be transported by advection and smoothed by dispersion are largely absent, and the assumption that SSC around the lake can be calculated independently at each location based on a one-dimensional (vertically averaged) simplification is valid.

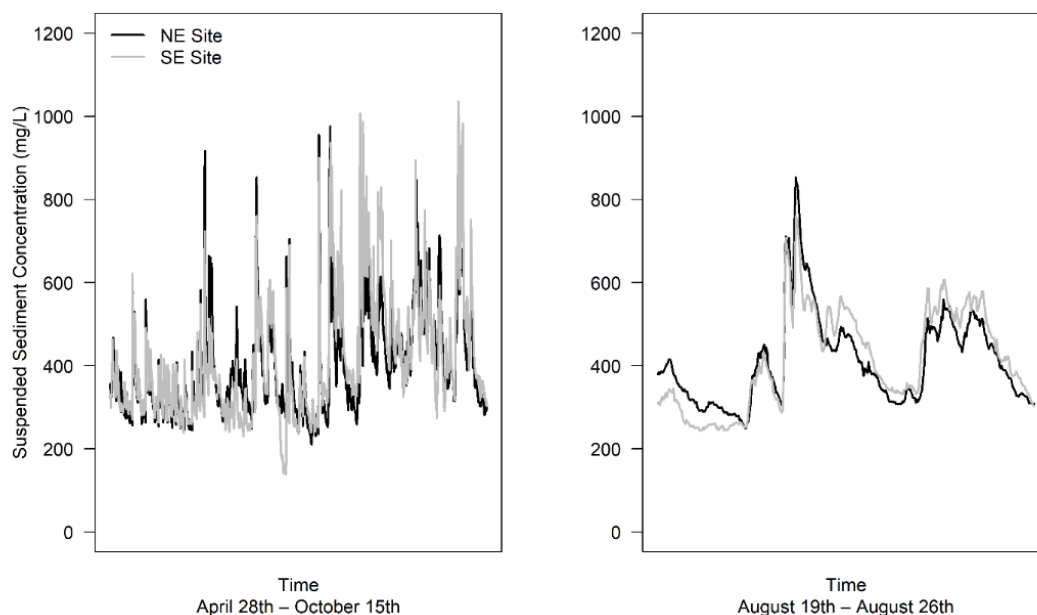


Figure 4.2. The graph on the left demonstrates how the two sites in Malheur Lake (NE and SE Sites;  $\approx 4.4$  km apart) respond similarly over long time scales (April 28<sup>th</sup> – October 15<sup>th</sup>) and the graph on the right demonstrates how these same sites also respond similarly to events on shorter time scales (August 19<sup>th</sup> – August 26<sup>th</sup>).

### Wind Resuspension Model - Overall

The wind resuspension model was constructed in STELLA 10.0.6 (ISEE Systems, Inc. Lebanon, NH USA<sup>9</sup>), and employs nine governing equations to quantify the physical processes of waves and the subsequent SSC (mg/L) in the water column based on morphological (i.e. water depth and wind fetch) and environmental variables (i.e. wind speed and wind direction; Ijima & Tang, 1966; USACE, 1984; Chapra, 2008; Table 4.1; Figure 4.3). We constructed two distinct erosion-deposition modules that worked additively to simulate the physical action of a heavier fraction of sediment (i.e. slow to respond to wind events and quick to fall out of suspension) and a lighter fraction of sediment (i.e. quick to respond to wind events and slow to fall out of suspension). The values used to simulate the nine major model parameters of the wind resuspension model (Table 4.1) were established through a combination of literature

<sup>9</sup> 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.

searches and model calibration using SSC data collected *in situ* at Malheur Lake (described in detail below).

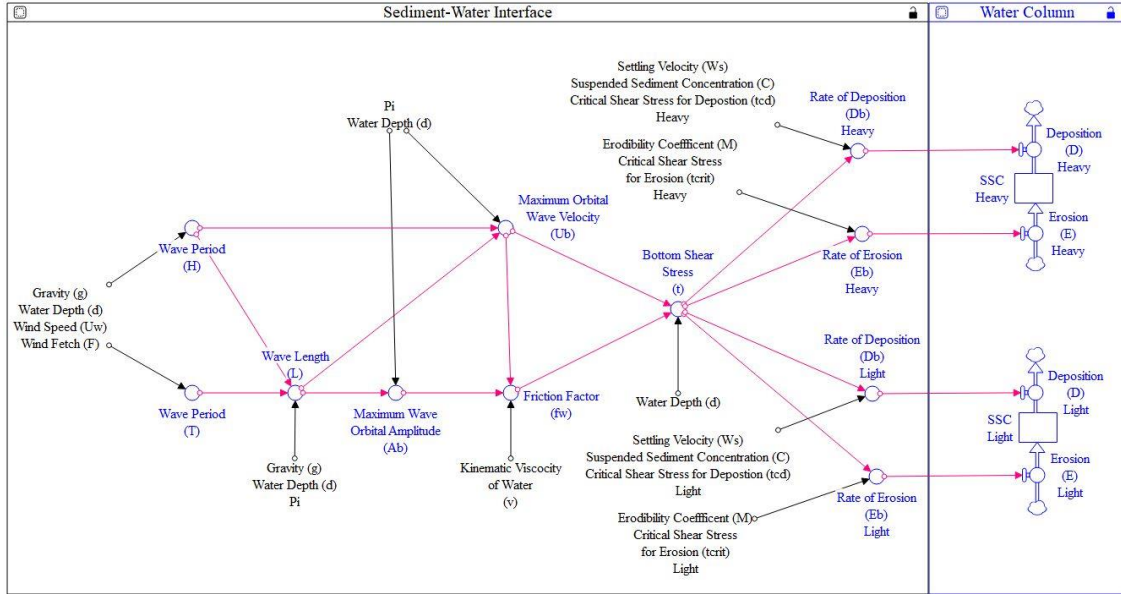


Figure 4.3. Conceptual diagram of the wind resuspension model. The thin black lines denote the input locations of the model parameters (text) into the nine governing equations (blue circles), the thin red lines denote the flow of values through the model, the valves (large blue arrows) depict flow of sediment into or out of the water column, and the boxes (blue) represent the suspended sediment concentration (SSC; mg/L) in the water column. The SSC is made up of two distinct fractions of sediment (i.e. heavier particles (heavy) and lighter particles (light)).

### Wind Resuspension Model – Equations and Coefficients

We calculated wave height ( $H$ ; m), wave period ( $T$ ; s), and wavelength ( $L$ ; m) as:

$$H = \left( \frac{U_w^2}{g} \right) 0.283 \tanh \left[ 0.530 \left( \frac{gd}{U_w^2} \right)^{0.75} \right] \tanh \left\{ \frac{0.0125 \left( \frac{gF}{U_w^2} \right)^{0.42}}{\tanh \left[ 0.530 \left( \frac{gd}{U_w^2} \right)^{0.75} \right]} \right\} \quad (1)$$

$$T = \frac{2\pi U_w}{g} 1.2 \tanh \left[ 0.833 \left( \frac{gd}{U_w^2} \right)^{0.375} \right] \tanh \left\{ \frac{0.077 \left( \frac{gF}{U_w^2} \right)^{0.25}}{\tanh \left[ 0.833 \left( \frac{gd}{U_w^2} \right)^{0.375} \right]} \right\} \quad (2)$$

$$L = \frac{gT^2}{2\pi} \tanh \left[ \left( \frac{2\pi d}{\frac{gT^2}{2\pi}} \right)^{0.75} \right]^{0.67} \quad (3)^{10}$$

where  $d$  is depth (m),  $g$  is gravity ( $\text{m/s}^2$ ),  $U_w$  is wind speed (m/s), and  $F$  is wind fetch length (m; CERC, 1984).

We calculated bottom shear stress ( $\tau$ ;  $\text{N/m}^2$ ) as:

$$\tau = \frac{1}{2} \rho f_w U_b^2 \quad (4)$$

where  $p$  is water density ( $\text{mg/mL}$ ),  $f_w$  is friction factor, and  $U_b$  is the maximum wave orbital velocity ( $\text{cm/s}$ ; Luettich et al., 1990).

The friction factor ( $f_w$ ) is:

$$f_w = 2 \left( \frac{U_b A_b}{\nu} \right)^{-0.5} \quad (5)$$

where  $A_b$  is the maximum wave orbital amplitude, and  $\nu$  is the kinematic viscosity of water ( $\text{m}^2/\text{s}$ ).

The maximum wave orbital amplitude ( $A_b$ ) and maximum orbital wave velocity ( $U_b$ ) is (Dyer, 1986):

$$A_b = \frac{1}{2 \sinh \left( \frac{2\pi d}{L} \right)} \quad (6)$$

$$U_b = \frac{\pi H}{T \sinh \left( \frac{2\pi d}{L} \right)} \quad (7)$$

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<sup>10</sup>  $\frac{gT^2}{2\pi}$  is the deep water wavelength calculation ( $L_o$ )



The rate of erosion ( $E_b$ ; kg/m<sup>2</sup>/s) is calculated (Partheniades, 1965):

$$E_b = \begin{cases} 0, & \tau \leq \tau_{crit} \\ M \left( \frac{\tau}{\tau_{crit}} - 1 \right), & \tau > \tau_{crit} \end{cases} \quad (8)$$

where  $M$  is erodibility coefficient (kg/m<sup>2</sup>/s) and  $\tau_{crit}$  is critical shear stress for erosion (N/m<sup>2</sup>).

The rate of deposition ( $D_b$ ; kg/m<sup>2</sup>/s) is calculated (Krone, 1962; Partheniades, 1965; Mehta & Partheniades, 1975):

$$D_b = \begin{cases} 0, & \tau \leq \tau_{crit} \\ W_s C \left( 1 - \frac{\tau}{\tau_{cd}} \right), & \tau > \tau_{crit} \end{cases} \quad (9)$$

where  $W_s$  is settling velocity (m/s),  $C$  is suspended sediment concentration (g/cm<sup>3</sup>), and  $\tau_{cd}$  is critical shear stress for deposition (N/m<sup>2</sup>).

Table 4.1. Values of model parameters with the letters  $H$  and  $L$  denoting parameters calibrated to simulate the heavier and lighter sediment fraction respectively.

Symbol	Parameters	Model Component	Values	Units	Calibrated
$g$	Gravity	Wave Calculations	9.8	m/s <sup>2</sup>	N
$\nu$	Kinematic Viscosity of Water	Friction Factor	0.9	m <sup>2</sup> /s	N
$\rho$	Water Density	Wave Shear Stress	1	g/ml	N
$w_s (H)$	Settling Velocity	Deposition Rates	0.00003	m/s	Y
$w_s (L)$	Settling Velocity	Deposition Rates	0.000000975	m/s	Y
$M (H)$	Erodibility Coefficient	Resuspension Rates	0.00000095	kg/m <sup>2</sup> /s	Y
$M (L)$	Erodibility Coefficient	Resuspension Rates	0.00000012	kg/m <sup>2</sup> /s	Y
$\tau_{crit} (H)$	Critical Shear Stress of Erosion	Resuspension Rates	0.02	N/m <sup>2</sup>	Y
$\tau_{crit} (L)$	Critical Shear Stress of Erosion	Resuspension Rates	0.01	N/m <sup>2</sup>	Y
$\tau_{cd} (H)$	Critical Shear Stress of Deposition	Deposition Rates	0.04	N/m <sup>2</sup>	Y
$\tau_{cd} (L)$	Critical Shear Stress of Deposition	Deposition Rates	0.4	N/m <sup>2</sup>	Y

### Wind Resuspension Model - Environmental and Morphological Variables

To make the model spatially explicit, a grid was overlaid (300 m<sup>2</sup>) in ArcGIS (ArcGIS; ArcMap Version 10.5; Environmental Systems Research Institute, Redlands, California, USA<sup>1</sup>), which enabled the quantification of environmental and morphological input variables throughout the lake. A grid cell size of 300 m<sup>2</sup> was used to provide the necessary topographical detail (i.e.

dikes, islands, variable water depths, etc.) while not adversely affecting computational time (total cells = 2560).

An application to calculate the wind fetch (m) was applied to each grid cell (Rohweder et al., 2008). The wind fetch was calculated at the centroid of each grid cell by taking the mean distance of nine radials at 3-degree increments to the shoreline and then repeated in 10 degree increments around a 360-degree arc. A water depth at the centroid of each grid cell was established using a digital elevation model DEM (10 m: Fusion – LiDAR and Ground Truth Survey) created by the USFWS (D. Craver, U.S. Fish and Wildlife Service, Portland OR, *unpublished data*). Wind speed and direction data were collected at a permanent USGS meteorological station (Station ID# 432046118503200; height = 3.26 m) on the northwest shoreline of Malheur Lake (30 minute intervals; Dyer, 1986). The wind speed data was adjusted to 10 m, which is the standard wind collection height, using the elevation adjustment equation:

$$U_A = U \left( \frac{10}{z} \right)^{\frac{1}{7}} \quad (10)$$

where  $U_A$  is the adjusted wind speed (m/s),  $U$  is the wind speed (m/s), and  $z$  is height (m) of the meteorological station (CERC, 1984; Kundu & Cohen, 2008).

The water depth and wind fetch variables were computed at three separate lake elevations in order to incorporate inter-annual variability in the lake area. These variables were computed at a lake elevation of 1247.75 m (average depth  $\approx$  0.13 m; max depth  $\approx$  0.26 m; lake area  $\approx$  3,663 ha), 1248.25 m (average depth  $\approx$  0.35 m; max depth  $\approx$  0.76 m; lake area  $\approx$  11,071 ha), and 1248.75 m (average depth  $\approx$  0.58 m; max depth  $\approx$  1.26 m; lake area  $\approx$  19,952 ha).

### **Suspended Sediment Concentration**

The continuous SSC data collected over three years (2017-2019) in Malheur Lake was used to calibrate and corroborate the wind resuspension model, however, during model calibration, there were noticeably multiple distinct fractions to the SSC data. For instance, the SSC data suggest a fraction (lighter fraction) that was slow to respond to decreases in wind speed, while another (heavier fraction) responded nearly instantaneously to decreases in wind speed. Based on this observational data along with a phytoplankton surrogate data (chlorophyll a – continuous sonde data) collected *in situ*, SSC was separated into three fractions (phytoplankton and a heavier and lighter detrital fractions; *unpublished data*: Figure 4.4).

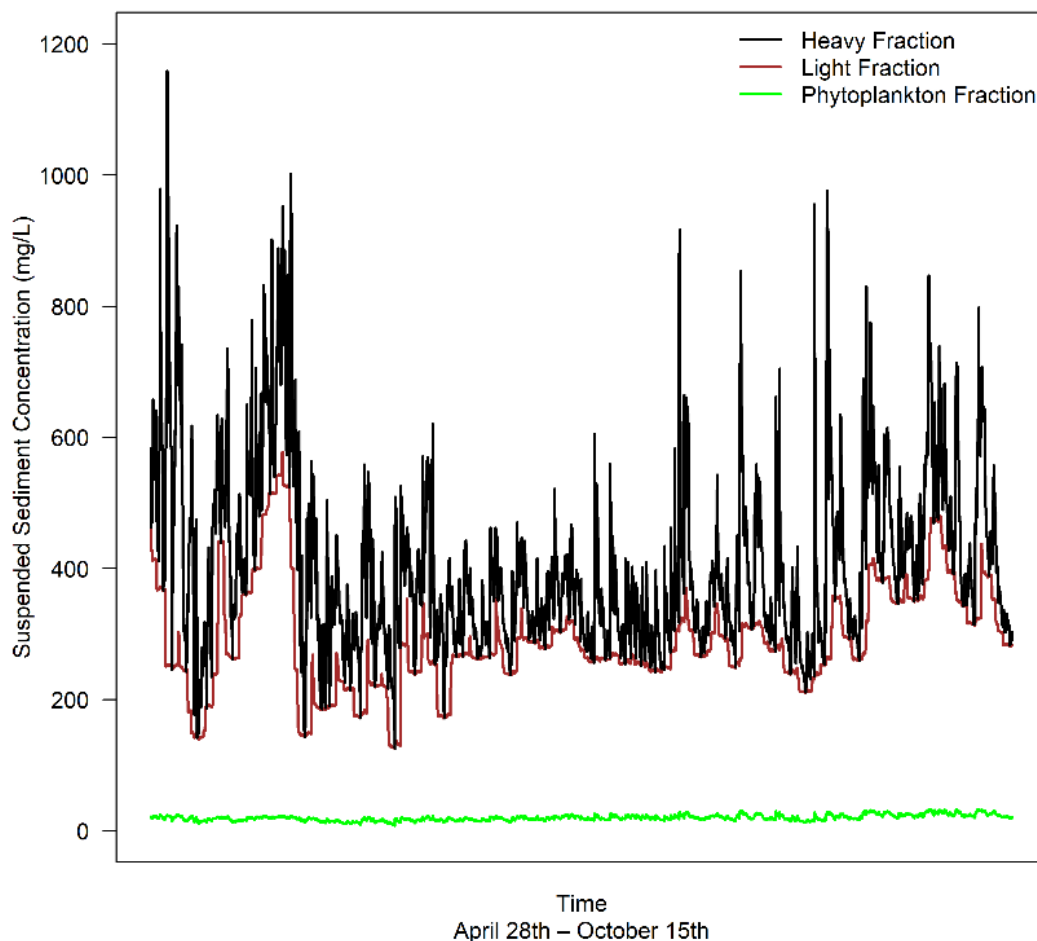


Figure 4.4. Graphical display demonstrating the three distinct fractions that make up the suspended sediment concentration (SSC; mg/L) in the water column in Malheur Lake. The green line denotes a phytoplankton fraction (derived via stoichiometry; *unpublished data* Tamara Wood USGS), the brown line denotes a lighter fraction (slow to fall out of suspension), and the black line denotes the heavier fraction of the SSC (quick to fall out of suspension).

### Model Evaluation

The wind resuspension model was evaluated to determine model efficiency, by comparing observed (SSC; mg/L; collected *in situ*) and predicted values via root mean square error (RMSE), normalized root mean square error (NRMSE), and mean absolute error (MAE). The RMSE described the variance between the two sets of data (observed vs. predicted) and is calculated as:

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^N (\hat{y}_i - y_i)^2} \quad (11)$$

where  $N$  is the total data points,  $\hat{y}_i$  is the modeled data values, and  $y_i$  is the observed data values. The RMSE aides in determining the amount of error in the predicted output, with values closer to zero indicating a good model fit (Chung et al., 2009). We used a normalized RMSE (NRMSE) to determine the relative difference (%) between the observed and predicted measurements. The normalized NRMSE is calculated:

$$NRMSE = \frac{RMSE}{(y_i \text{ Max} - y_i \text{ Min})} \quad (12)$$

where  $M$  is the mean of the observed measurements. Previous research has demonstrated that the model fit is considered excellent when the NRMSE < 10%, good if the NRMSE < 20%, fair if the NRMSE < 30%, and poor if the NRMSE > 30% (Jamieson et al., 1991; Liu et al., 2011).

The mean absolute error (MAE) was also used to measure model fit, and differs from the RMSE in that the MAE demonstrates a linear difference (error between values weighted equally) between observed and predicted values unlike RMSE which minimizes extreme values. The MAE is calculated:

$$MAE = \frac{1}{N} \sum_{i=1}^N |\hat{y}_i - y_i| \quad (13)$$

where again, values closer to zero indicate a good model fit (Chung et al., 2009).

### Model Performance

To ensure model accuracy and generalizability, observational SSC data collected *in situ* was compared to model outputs to determine the capacity for the model to predict SSC. While a majority of the wind resuspension model uses equations governed by the laws of physics, the

deposition and erosion equations are based on the sediment dynamics in the modeled lake erodibility coefficient ( $M$ ), settling velocity ( $W_s$ ), critical shear stress for erosion ( $\tau_{crit}$ ), critical shear stress for deposition ( $\tau_{cd}$ ), and thus it is necessary to parameterize these equations with lake specific model coefficients. Therefore, the wind resuspension model was simulated using the environmental data (wind speed and wind direction) collected at the meteorological station and the continuous SSC data collected at the NE site in 2019 (most continuous SSC data throughout project).

Due to the unique construction of the wind resuspension model, in which there are two distinct erosion-deposition modules, these two modules were first calibrated individually. For each module, four model coefficients ( $M$ ,  $W_s$ ,  $\tau_{crit}$ ,  $\tau_{cd}$ ) were systematically shifted, using the output RMSE and MAE values. Once the lowest RMSE and MAE values were obtained for each individual module, the module were next corroborated in combination, using data collected during 2017 – 2019 at both the NE and SE sites. The RMSE, NRMSE, and MAE values were calculated for each year and site to demonstrate the overall model fit to multiple sets unique environmental data.

## **Model Application**

### Heuristic Model

A heuristic modeling approach was undertaken to better understand the basic physical processes of wind resuspension at the scale of Malheur Lake (large, shallow, long wind fetches). The model was used to examine how wind speed (0 - 12 m/s), wind fetch (0 - 10,000 m) and water depths (0 – 1 m) affect the overall bottom shear stress ( $\tau$ ) in Malheur Lake. These results were used to determine at which point (wind fetch distance, water depth, and wind speed), a critical shear stress is exceeded and sediment begins to be suspended into the water

column. The threshold we use to determine this point was the  $\tau_{\text{crit}}$  for both the lighter and heavier erosion-deposition modules ( $\tau_{\text{crit}} = 0.01$  and  $0.02$  respectively).

### Baseline Model

Baseline models were simulated at the three distinct lake elevations (1247.75, 1248.25, 1248.75 m) using meteorological data (wind speed and wind direction) collected in 2018 (March 1<sup>st</sup> – November 30<sup>th</sup>; ice off period). These first baseline simulations enabled me to identify how the unique morphological drivers (i.e. lake area, water depth, and wind fetch) at each lake elevation was influenced by similar environmental data (i.e. wind speed and wind direction; Figure 4.5). Total SSC, Average SSC, and percent change in SSC (%  $\Delta$ SSC) were quantified for each simulation in order to enable me to compare model outputs between the three lake elevations.

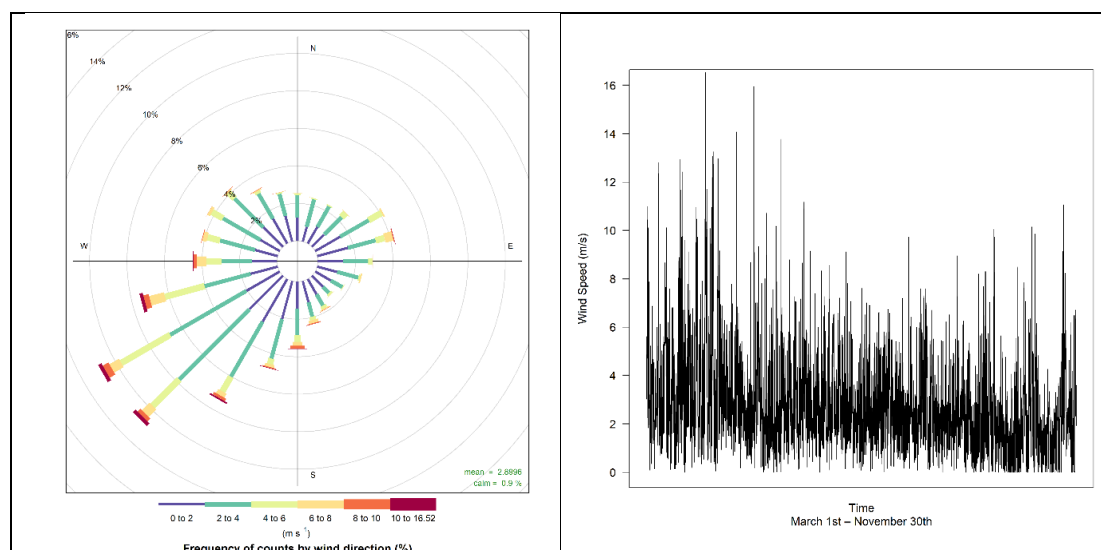


Figure 4.5. Wind speed and wind direction during the 2018 baseline model simulation. The graph on the left is a wind rose that demonstrates the predominant wind direction and the graph on the right demonstrates the wind speed over the simulated time period. The data used in this simulation was collected at the permanent USGS meteorological station (Station ID# 432046118503200) on the northwest shoreline of Malheur Lake (30 minute intervals: March 1<sup>st</sup> – November 30<sup>th</sup>).

### Wave Reduction Barrier Scenarios

Wave reduction barriers (WRB) were simulated because of their ability to decrease wind fetch lengths and reduce the bottom shear stress in the area immediately following the WRB. The WRB simulates a solid feature that extends from the substrate, through the water column, extending out of the water, resulting in a complete reduction in wave transmission. Each simulated WRB is 900 m (5 cells) and located in the deepest part of the lake, perpendicular to the predominant wind direction (230 degrees). The WRB were placed within the boundary of the lowest lake area scenario (1247.75 m), in order for the WRB to be effective at all lake elevations scenarios (1247.75, 1248.25, 1248.75 m). The three WRB treatment scenarios were: 1) one WRB (1 WRB), 2) three WRB (3 WRB), and 3) six WRB (6 WRB). Similar to the baseline scenarios, the WRB scenarios were simulated at the three distinct lake elevations (1247.75, 1248.25, 1248.75 m) using the meteorological data (wind speed and wind direction) collected in 2018 (March 1<sup>st</sup> – November 30<sup>th</sup>). The baseline models simulated in the previous section were used to compare the efficacy of the WRB scenarios, thus Total SSC, Average SSC, and percent change in SSC (%  $\Delta$ SSC) were quantified for each simulation in order to facilitate this comparison.

## **Results**

### **Model Performance**

Model predictions exhibited strong correspondence with the observed data (Figure 4.6; Table 4.3). The heavy sediment calibrated model had an RMSE of 102.53 mg/L, MAE of 70.37 mg/L, and a NRMSE of 14.40%, while the light sediment calibrated model had an RMSE of 98.31 mg/L, MAE of 74.34 mg/L, and a NRMSE of 22.52%. The model validation (combination of heavy and light fraction) had an average RMSE of 254.91 mg/L, MAE of 189.36 mg/L, and NRMSE of 19.30%, which is considered a fair model fit.



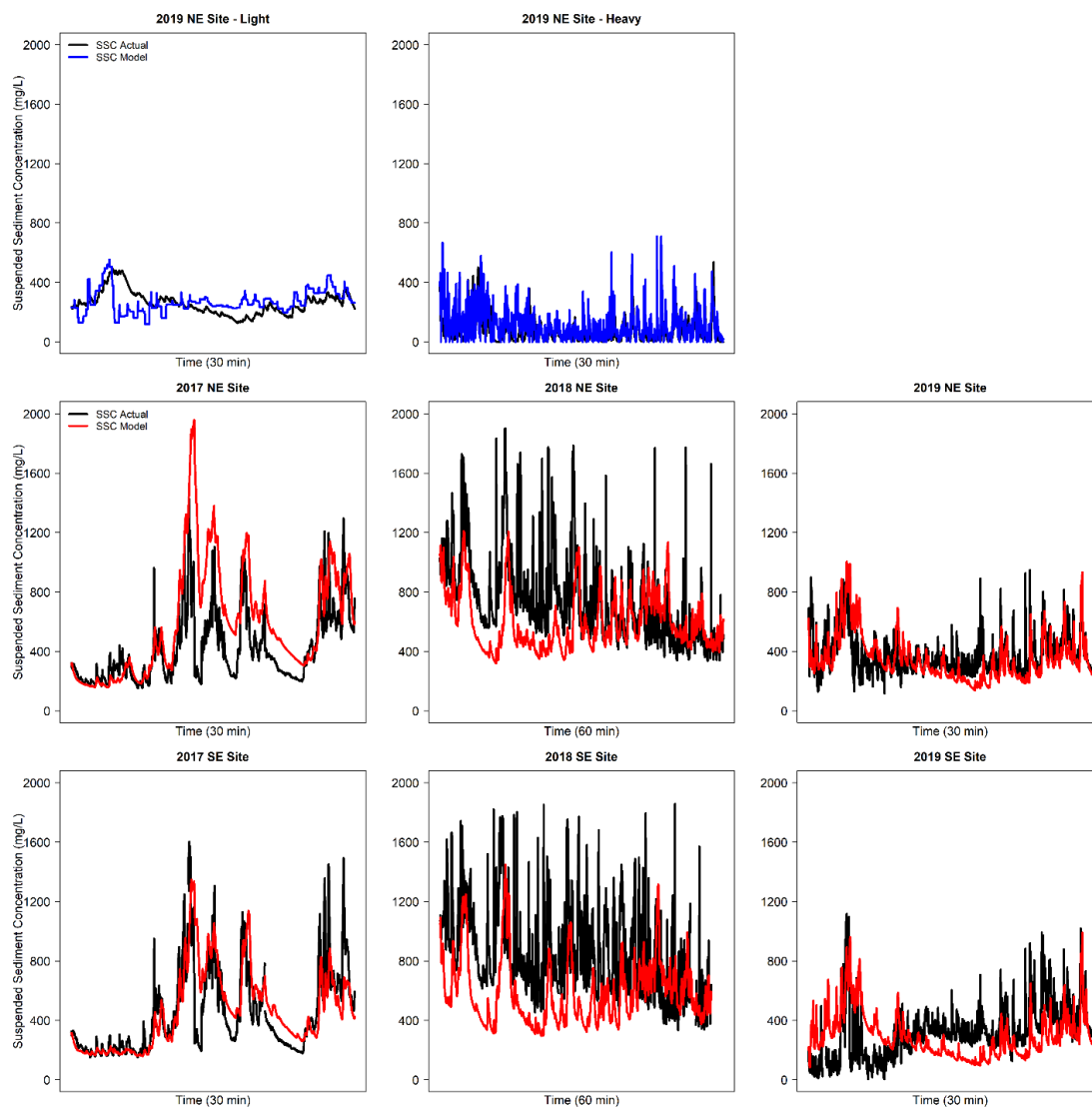


Figure 4.6. Model calibrations and validations for both sites over all three years of data collection. The black lines denote the continuous suspended sediment concentration (SSC; mg/L) data collected in Malheur Lake during the three sampling years at two separate locations (NE and SE sites). The blue line denotes the individually calibrated models (heavy and light) while the red lines denote the corroborated model outputs. The 2017 calibration was simulated using data collected August 31<sup>st</sup> – November 7<sup>th</sup>, the 2018 calibration was simulated using data collected April 20<sup>th</sup> – August 1<sup>st</sup>, 2019 calibration and validation was simulated using data collected April 28<sup>th</sup> – October 15<sup>th</sup>.

Table 4.2. Model calibration and validation results. The two distinct erosion-deposition modules (heavy and light) were individually calibrated using the continuous 2019 suspended sediment concentration (SSC; mg/L) with the data separated into two distinct fractions (heavy and light). The overall model was then validated using the additive outputs from the two erosion-deposition models against data from 2017-2019 at both sites (NE and SE Sites).

Metrics				NE			SE		
	2019 (H)*	2019 (L)*	2017	2018	2019	2017	2018	2019	
RMSE	102.53	98.31	303.02	301.50	131.97	195.83	394.59	202.56	
MAE	70.37	74.34	204.26	223.25	95.42	126.15	318.31	168.77	
NRMSE	14.40	22.52	23.81	19.21	15.32	13.46	25.84	18.16	
N	8083	8083	2286	2297	8083	2274	2149	7950	
Max	711.87	553.93	1425.39	1902.61	978.88	1603.88	1859.20	1118.14	
Min	0	117.41	152.61	333.31	117.41	149.33	332.29	2.83	
Avg	112.86	267.18	418.25	738.06	380.04	448.78	848.23	324.38	

\* denotes the calibration

## Model Application

### Heuristic Model

The heuristic modeling outputs demonstrated that shallow areas of Malheur Lake (0.25 m) are more susceptible to wind resuspension at lower wind speeds and intermediate wind fetch lengths than the deeper regions. For instance, the heuristic modeling outputs demonstrated that at a wind speed of 2 m/s, regions of the lake that are  $\leq 0.25$  m surpassed the critical shear stress of erosion ( $\tau_{crit}(L) = 0.01 \text{ N/m}^2$ ) threshold at a wind fetch  $>1000$  m and the critical shear stress of erosion ( $\tau_{crit}(H) = 0.02 \text{ N/m}^2$ ) threshold at a wind fetch  $>2000$  m, whereas regions  $\geq .50$  m did not cross the same thresholds until  $>2800$  and  $>5800$  m respectively (Figure 4.7). While the shallow regions are also susceptible to resuspension at high wind speeds, simulations demonstrated that deeper regions ( $> 0.50$  m) had greater bottom shear stress at these higher wind speeds. For instance, the model outputs demonstrated that at a wind speed of 12 m/s and a wind fetch of 10,000 m, regions of the lake that are 0.25 m had a bottom shear stress ( $\tau$ ) of  $0.15 \text{ N/m}^2$  while regions of the lake that are 1 m had a bottom shear stress ( $\tau$ ) of  $0.27 \text{ N/m}^2$ .

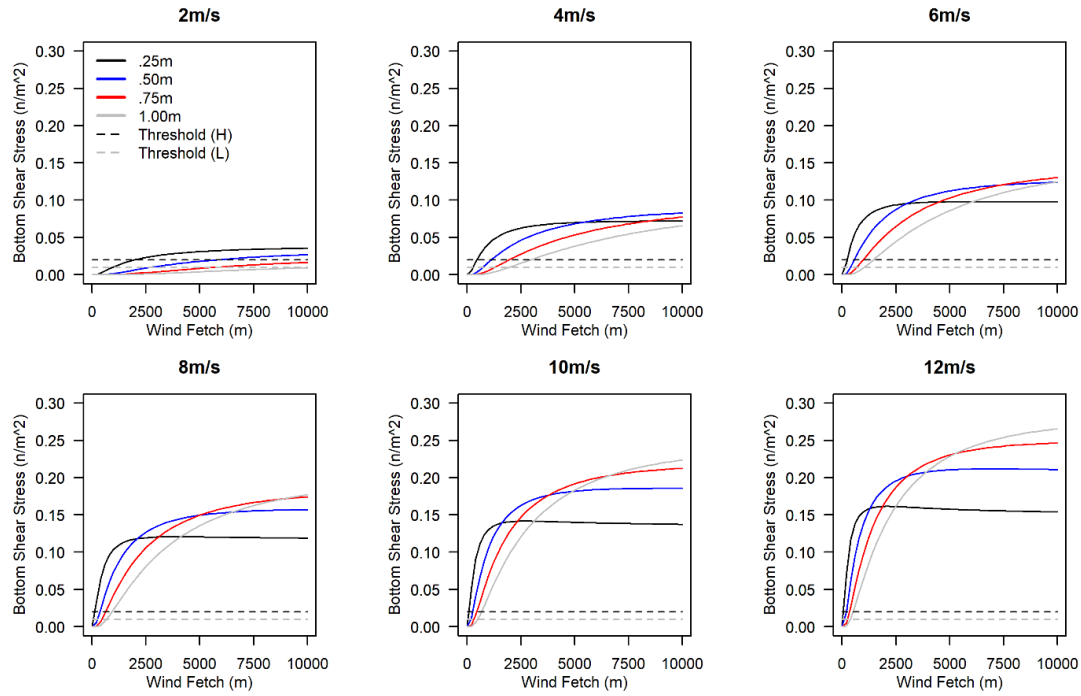


Figure 4.7. Heuristic model outputs demonstrating the forces exerted along the sediment (bottom shear stress ( $\tau$ );  $\text{N/m}^2$ ) at different depths (0.25 – 1.0 m), wind fetches (0 – 10,000 m), and wind speeds (2 - 12 m/s).

### Baseline Model

The baseline models were simulated using data from 2018 (March 1<sup>st</sup> – November 30<sup>th</sup>; ice off period), at multiple lake elevations (1247.75, 1248.25, 1248.75 m), and thus the outputs demonstrated how the overall SSC in Malheur Lake fluctuates based on shifts in the environmental drivers (i.e. wind speed, wind direction) as well as shifts in the morphological drivers (water depth and wind fetch). The overall average SSC decreases as the lake area increases (Figure 4.8; Table 4.3; 1247.75 = 444.0, 1248.25 = 235.52, and 1248.75 m = 168.88 mg/L), and an examination of only cells encompassing the lowest lake level (1247.75 m), showed a reduction in the average SSC with increasing lake area (1247.75 = 444.0, 1248.25 = 193.1, and 1248.75 m = 97.0 mg/L).

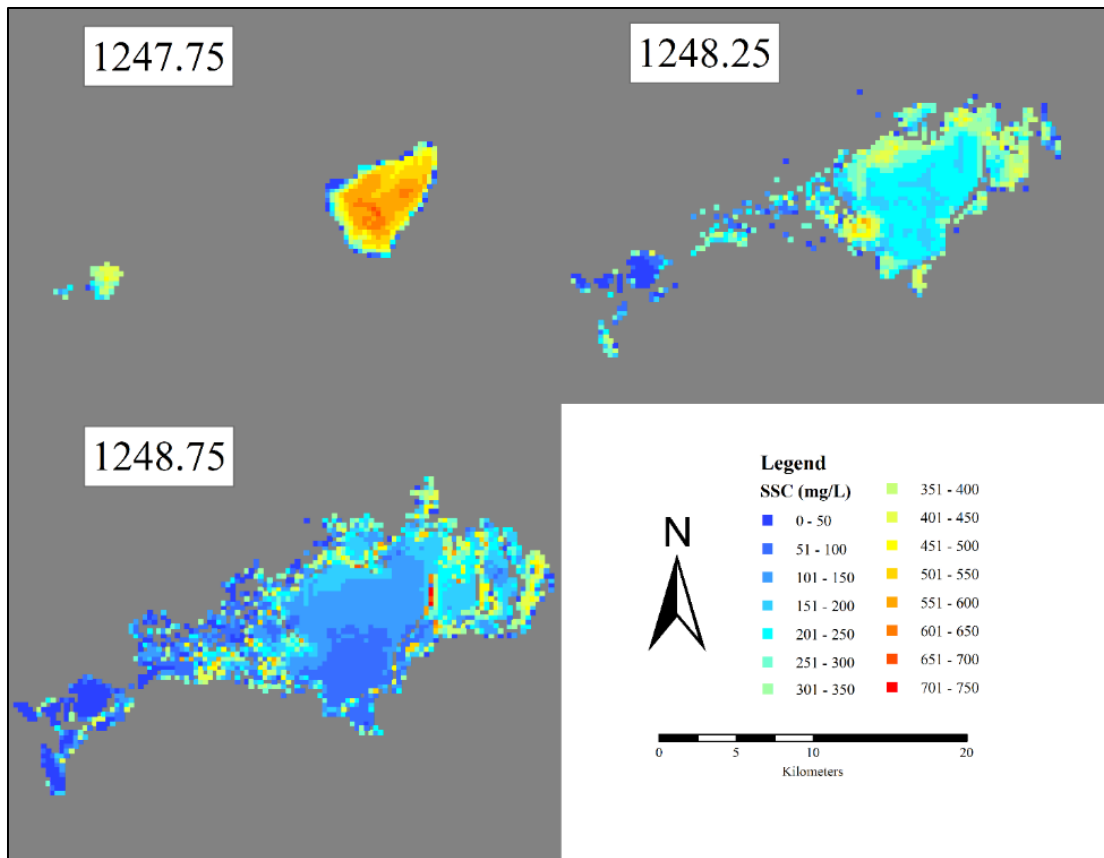


Figure 4.8. Maps illustrating the average suspended sediment concentration (SSC; mg/L) for each cell throughout Malheur Lake at the three distinct lake elevations (1247.75, 1248.25, 1248.75; Table 4.3).

#### Wave Reduction Barrier Scenarios

Model simulations demonstrated large reductions in the overall SSC for all WRB scenarios (WRB 1, 3, 6) and across all lake elevations (Table 4.3; Figure 4.9). Simulations showed the largest reduction in the overall SSC were the 6 WRB scenario at the lowest lake elevation (1247.75 m). Simulations also display a decrease in the efficacy of WRB as the number of WRB and lake elevation increase (%  $\Delta$  SSC; 1247.75 6 WRB = 21.76% vs. 1248.75 6 WRB = 14.91%; Table 4.3).

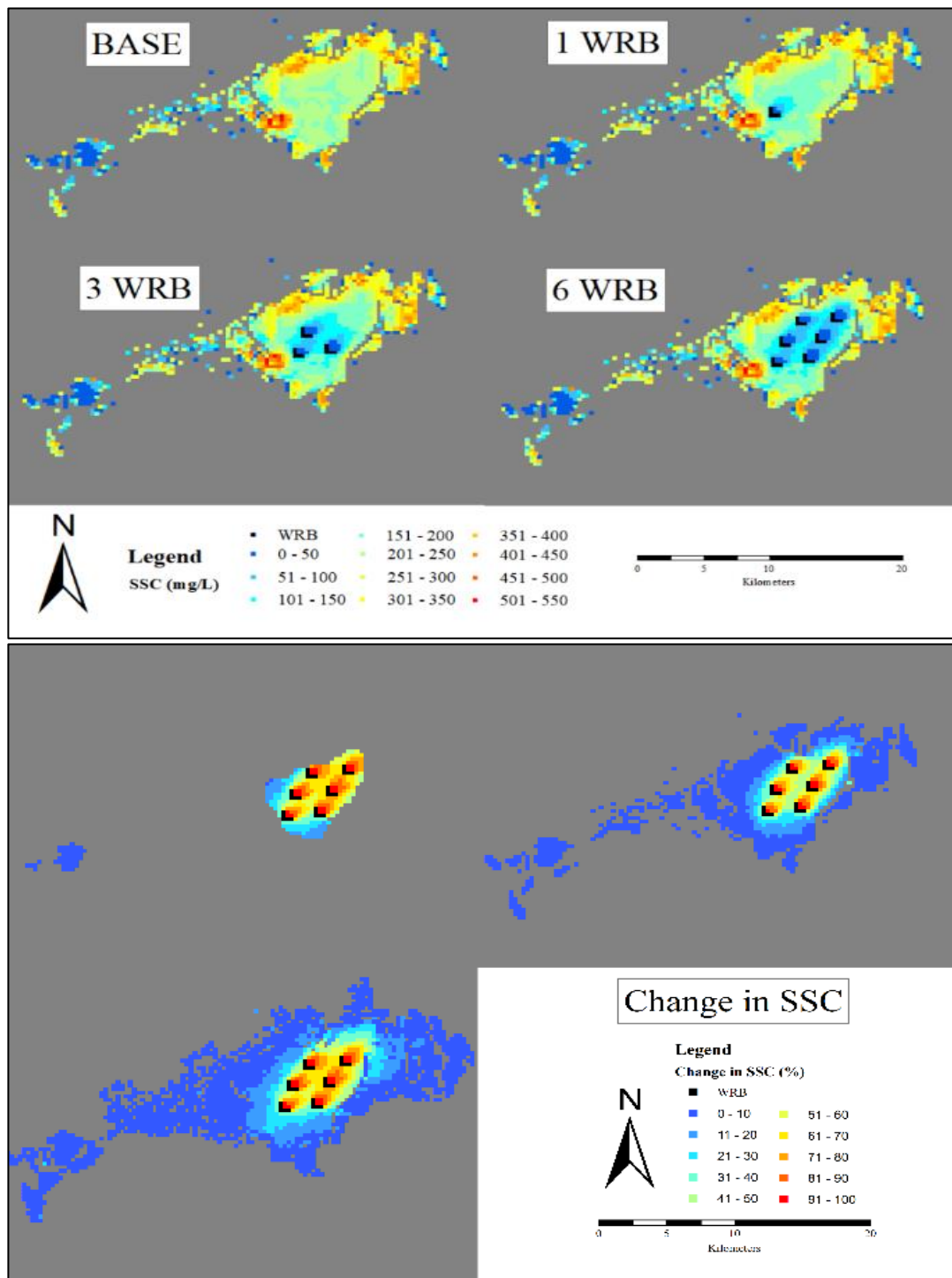


Figure 4.9 Maps illustrating the reduction in the average suspended sediment concentration (SSC; mg/L) due to the implementation of WRB. The collection of maps in the top area display how the overall SSC is effected by WRB at similar lake elevations (1248.25 m). The collection of maps in the bottom area display the overall change in SSC brought about by 6 WRB implemented at three different lake elevation (1247.75, 1248.25, 1248.75 m).

Table 4.3. Table displaying simulation outputs for the wave reduction barriers (WRB) scenarios. Table A shows the average suspended sediment concentration (SSC; mg/L) concentration overall average SSC for each lake elevation and WRB scenarios. Table B shows the average percent change per cell in comparison to the baseline model. Table C shows the average percent change per cell per WRB. The conditional formatting in each table is meant to more easily identify the higher (red) and lower (blue) values.

A	Average SSC	BASE	1 WRB	3 WRB	6 WRB
	1247.75	444.04	430.28	380.83	324.13
	1248.25	235.52	226.88	212.1	196.19
	1248.75	168.88	165.15	158.07	149.48
B	% Δ SSC	BASE	1 WRB	3 WRB	6 WRB
	1247.75	-	2.81%	11.38%	21.76%
	1248.25	-	3.95%	10.82%	17.67%
	1248.75	-	3.33%	9.18%	14.91%
C	% Δ SSC / WRB	BASE	1 WRB	3 WRB	6 WRB
	1247.75	-	2.81%	3.79%	3.63%
	1248.25	-	3.95%	3.61%	2.95%
	1248.75	-	3.33%	3.06%	2.49%

## Discussion

Mechanistic models are often used to evaluate restoration actions influencing complex ecosystems, thus enabling an assessment of the consequences of proposed action alternatives before investing limited resources (Stone & Andreu, 2017; Spies et al., 2017; Cai et al., 2018). Here we evaluated the physical dynamics of a large, shallow lake ecosystem (Malheur Lake, Oregon) with a wind resuspension model developed to incorporate two distinct erosion-deposition modules accounting for two weight classes of potentially suspended particles. The model allowed us to assess how morphological and environmental drivers at different lake areas affect overall suspended sediment concentrations (SSC). Simulations suggested that wind driven sediment suspension is the main driver of SSC and that wave reduction barriers (WRB) could be used to reduce the deleterious effects of the winds energy and decrease the overall SSC in the water column (Figure 4.9). However, our results also suggest that due to the large-shallow nature of Malheur Lake, the implementation of WRB would need to be extensive in order to fully overcome the wind driven sediment resuspension.

Heuristic modeling undertaken in this study identified regions of the lake that may be most susceptible to wind resuspension based on water depth, wind fetch, and wind speed. For instance, these simulations demonstrated that shallow areas ( $\leq 0.25$  m) were more susceptible to wind resuspension at lower wind speeds and intermediate wind fetches. This can be problematic in a region such as southeastern Oregon where windy conditions are more or less constant, with outputs from a local meteorological station (USGS Station ID# 432046118503200) indicating calm conditions (wind speed = 0 m/s) only 0.9 % of the time during the 2018 simulation period (March 1<sup>st</sup> – November 30<sup>th</sup>; Figure 4.9). Model outputs also demonstrated that the deeper regions ( $\approx 1$  m) in the lake are more capable of greater wave forces because the waves can more fully form, thus exerting greater bottom shear stress ( $\tau$ ).

The baseline model simulations clearly reveal that fluctuations in lake area (increasing/decreasing lake elevation) can cause large disparities in the average SSC in Malheur Lake (Figure 4.7; Table 4.3). For instance, simulations indicate that when the lake elevation is at 1247.75 m, the sediment resuspension is increased, with SSC values averaging 444.0 mg/L, while this same area (3,663 ha) at the higher lake elevations (1248.25 and 1248.75 m) has SSC values that average 193.1 and 97.0 mg/L respectively. Our observation of a greater average SSC at lower lake elevations runs counterintuitive to findings of many studies of wind resuspension in shallow lakes, where longer wind fetches generally correspond to greater wave heights, greater bottom shear stresses, and ultimately greater SSC in the water column (CERC, 1984; Carper & Bachmann, 1984; Janssen, et al., 2014). The unique morphometry of Malheur Lake, however, is responsible for our findings, as it is extremely shallow with a greater proportion of area that is more susceptible to wind resuspension at lower wind speeds and intermediate wind fetches. This was evident with model simulations that illustrated how shallow ( $\approx 0.25$  m) regions of Malheur Lake are susceptible to wind resuspension at low wind speeds of 2 m/s and intermediate wind fetches  $\approx 1000$  m, whereas deeper regions ( $\geq 0.50$  m) are

not susceptible to wind resuspension unless wind fetches are much longer (>2800 m; Figure 4.6).

The WRB scenario simulations indicated an effect of the WRB on the average SSC in the water column, with the addition of 6 WRB resulting in an overall reduction in the SSC by 119.91, 39.33, and 19.4 mg/L at the three distinct lake elevations (1247.75, 1248.25, 1248.75 m respectively). These outputs suggest that WRB could be used in some capacity to aid restoration efforts targeting a reduction in SSC in order to promote the growth of aquatic macrophytes in Malheur Lake. However, WRB simulations at different lake elevations, demonstrated a diminishing return on the reduction of SSC as the lake area increased (Table 4.3). The diminishing return is due to a combination of lake area, wind fetch length, and water depths. For instance, as the lake area increases, so do the wind fetches (all directions), whereas at the lowest lake elevation (1247.75 m) the effect of the WRB can overwhelm the system and reduce the average SSC throughout the lake.

While we have identified wind resuspension as a driver of the overall SSC in Malheur Lake, a biological agent, Common Carp (*Cyprinus carpio*), which invaded Malheur Lake in the 1950's also potentially adds to the overall SSC in the water column (Ivey et al., 1998). The foraging behavior of Common Carp (hereafter "carp") adds sediment to the water column both directly via expelling sediment through their opercular slits as well as indirectly via loosening of the substrate, thus making the sediment more susceptible to wind resuspension (Callan & Sanderson, 2003; Scheffer et al., 2003; Penning et al., 2013). The amount of sediment that is added directly to the water column via carp has been identified experimentally as approximately proportional to the overall carp biomass, with an increase in the SSC from  $\approx 0$  to 80 mg/L as the overall carp biomass increases from  $\approx 0$  to 2000 kg/ha (Breukelaar et al., 1994). Based on carp population modeling in the system (Chapters 2 & 3; Pearson et al., 2019),



in which the median carp biomass outputs rarely exceeded 1000 kg/ha (1938-2018 simulated carp biomass  $\approx 573 \pm 367$  kg/ha, median  $\pm$  standard deviation), we can assume that the carp in Malheur Lake generally directly add  $< 80$  mg/L to the overall SSC in the water column. Thus, while carp likely add to the overall SSC in Malheur Lake, it is likely that carp only add a small fraction directly to the average SSC in the water column (2017-2019 average SSC  $\approx 526.3$  mg/L). While the sediment added directly to the water column via carp has been experimentally identified and can be roughly assumed in Malheur Lake, the amount of sediment that the carp indirectly add to the SSC via a loosening of the substrate is much less understood. Therefore, future research aimed at identifying the indirect effect that carp have on the overall SSC via loosening of the substrate could be useful to managers that may focus management actions (i.e. carp exclusion) on areas that are most susceptible to wind resuspension (i.e. long wind fetches and shallow depths).

While our model results demonstrate that WRB likely could be used to aid in the restoration of Malheur Lake, we were only able to find one article in which a WRB was used in an attempt to restore clear water conditions in a shallow lake. In Lake Taihu, China (lake area  $\approx 233,800$  ha and mean depth = 1.9 m), a large WRB ( $> 3$ km) was able to reduce the sediment resuspension within the treated area by 36.45%, with a concomitant 38.76% reduction in total phosphorus (Huang & Liu, 2009). While the WRB was successful at reducing the suspended sediment and total phosphorous, the phytoplankton biomass remained sufficiently high, and thus maintained the turbid state (Huang & Liu, 2009). In the context of the alternative stable states, this is an example in which the proposed restoration action is not robust enough to overcome the strong positive reinforcing feedback loops present in shallow lakes, pulling the overall aquatic environment towards the turbid state (May, 1977; Scheffer et al., 2001; Janssen, et al., 2014). Thus, management actions that use WRB could be more effective if other restoration actions are implemented as well, not only to overcome the reinforcing feedback

loops working towards the turbid state (i.e. wind resuspension, internal and external nutrient loading, invasive benthivorous fish species, etc.) but also initiate reinforcing feedback loops that work toward the clear state (wave reduction barriers, planting aquatic macrophytes, restricting benthivorous fish species, limiting external nutrients; Scheffer et al., 1993; Williams, 2005; Janssen, et al., 2014; Huang & Liu, 2009).

Whereas our modeling demonstrated that human-constructed wave reduction barriers may be used to decrease the overall SSC in Malheur Lake, there are other means of attaining the same ends. For instance, facilitating establishment of emergent vegetation in the lake could reduce wind-driven SSC, with results expected to vary among locations based on results of this work. Work in other systems has demonstrated that emergent vegetation can act to dissipate wave energy in shallow lakes, thus decreasing the winds forces and limiting resuspension. The rigid stems of emergent vegetation can dissipate the height of peak turbulence, and thus lower the frequency of resuspension events (increased wave dissipation with stem density; Horppila et al., 2013). Emergent vegetation has also been shown to have a large effect on reducing internal phosphorous loading, with emergent vegetation decreasing loading by 26 mg/m<sup>2</sup>/d (Horppila & Nurminen, 2005). Furthermore, we were unable to find a study that has demonstrated deleterious effects of carp on emergent vegetation, yet there are a large number of studies demonstrating the negative effect of carp on submergent vegetation both directly and indirectly (Crivelli, 1983; Lougheed et al., 1998; Miller & Crowl, 2006; Matsuzaki et al., 2007; Weber & Brown, 2009). Therefore, unlike submergent vegetation that is adversely affected by carp, emergent vegetation should be able to persist even in the presence of carp, and thus provide shelter from the forces of wind and potentially promote favorable growing conditions for submergent vegetation during years in which the carp biomass is low either via carp management actions or natural population fluctuations brought on by environmental variability (Chapter 2).

In the context of lake restoration, the use of emergent vegetation as a WRB could be viewed as a reinforcing feedback loop which in combination with other restoration actions (restricting benthivorous fish species, limiting external nutrients, etc.) may be able to shift Malheur Lake from the turbid to clear state. For instance, as described above, emergent vegetation can diminish the deleterious effects of wind/wave energy, and thus would likely increase the light in the water column, which may further promote the growth of more emergent or submergent vegetation (positive/reinforcing feedback loops). For this reason, reinforcing (positive) feedback loops are considered one of the areas of a system that are best leveraged and should be targeted to increase the likelihood of restoration actions. While reinforcing feedback loops are one of the best leverage points, balancing (negative) feedback loops are considered a poor area to target because balancing feedback loops are meant to be self-regulating, and thus have very little energy to make substantial changes to a system (Meadows, 2008). However, it is often the case that managers unknowingly focus substantial resources towards restoration actions that act as a balancing feedback loop on a system and thus are likely to fail. For instance, managers who focus solely on carp control as a restoration action are focusing efforts on a balancing feedback loop, in which the removal of carp acts to slow or limit the reinforcing feedback loop of carp recruitment, and therefore will likely never be successful as the sole means of restoration (Chapters 2 & 3; Pearson et al., 2019).

There are other factors that are outside of the control of managers that deserve consideration. For instance, changing regional climate conditions, including increasing prospects for regional droughts, are a concern in the future (Snyder et al., 2019). In the Malheur Lake ecosystem, antecedent hydrological events are also potentially important in determining the contemporary lake state. During the prolonged flooding in the 1980's, Malheur Lake increased to a lake area of  $\approx 51,500$  ha (average lake area = 19,200 ha) with a max depth of  $\approx 4.4$  m (avg max depth =

1.26 m), exceeding all previously instrumented recordings (Hostetler & Bartlein, 1990). These floods inundated the previously robust emergent vegetation stands for an extended period of time and under depths at which they may not have been able to survive, and thus once the flooding subsided, Malheur Lake was void of emergent vegetation except for a narrow ring around the lake. It has been hypothesized that the loss of emergent vegetation, specifically the rooted structures that act to secure the sediment is why Malheur Lake is now highly susceptible to wind resuspension (Hamilton et al., 1986).

Although the model developed in this study provided many useful insights into factors driving the emergence of turbid water conditions in Malheur Lake, it is important to highlight the uniqueness of this system, relative to studies of other shallow lakes. The calibration process undertaken in this chapter demonstrated how the characteristics of the sediment influenced the erosion and deposition parameters ( $M$ ,  $W_s$ ,  $\tau_{crit}$ ,  $\tau_{cd}$ ), and thus made the model individual to Malheur Lake. For instance, in review of other wind resuspension models, it is clear that there is a large range in parameter values between lakes, and this is likely due to their unique sediment compositions (organic and inorganic; Luettich et al., 1990; Jin & Ji, 2004; Chao et al., 2008; Lee et al., 2015; Liu et al., 2019; Table 4.4). While the validation section of this chapter demonstrates the generalizability of this model, it also demonstrates that there is a difference between the two sites (NE and SE) in which data was collected, and thus there is likely some spatial variability in sediment characteristics throughout Malheur Lake. The spatial variability in sediment characteristics, and likely in model parameter values is assumed to be due to periodic suspension and redistribution events that happen during large storm events (Zhu, 2008; Penning et al., 2013).

Table 4.4 Comparison of wind resuspension parameters.

Critical Shear Stress of Erosion ( $\tau_{crit}$ ; N/m <sup>2</sup> )	Critical Shear Stress of Deposition ( $\tau_{cd}$ ; N/m <sup>2</sup> )	Erodibility Coefficient (M; kg/m <sup>2</sup> /s)	Settling Velocity (ws; m/s)	Citation
0.02	0.04	0.00000095	0.00003	This Study ( <i>H</i> )
0.01	0.4	0.00000012	0.000000975	This Study ( <i>L</i> )
0.005	0.0005	0.000005	0.001	Liu et al., (2019)
0.216	0.18	0.000005	0.00001	Jin and Ji (2004)
0.02	0.01	0.00001	0.005	Chao et al., (2008)
0.02	0.18	0.0000034	0.02	Lee et al., 2015
--	--	--	0.022	Luetlich et al., 1990

Two factors that were not investigated in this model are how fluctuations in SSC ultimately effect the PAR and nutrient concentrations in the water column of Malheur Lake. However, the model as currently constructed could be used in the future to investigate these factors via an expansion of the model components. Nevertheless, the modeling conducted in this study has improved our overall understanding of the aquatic ecosystem of Malheur Lake and demonstrated how both morphological and environmental factors drive the overall SSC.

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## **Chapter 5: Conclusion**

In this dissertation, I used a mechanistic modeling approach to provide a greater understanding of the drivers of turbidity in Malheur Lake and demonstrated the efficacy of multiple restoration alternatives targeted at shifting the aquatic ecosystem from a turbid to a clear state. For instance, the Common Carp (*Cyprinus carpio*; hereafter “carp”) population dynamics modeling conducted in Chapters 2-3 demonstrated that restoration actions solely targeting the adult life stage (commercial harvest) are often unsuccessful because carp populations exhibit compensatory density dependence, in which demographic rates shift in response to population densities (Weber et al., 2016; Rose et al., 2001). Therefore, our modeling simulations demonstrated that management actions directed at suppressing carp populations should target multiple life-stages in order to overcome these compensatory responses. Furthermore, our modeling also demonstrated that managers can benefit from a better understanding of how environmental drivers may be affecting the carp population. For instance, carp populations in highly variable (water fluctuations) lakes and wetlands are likely more affected by the interactions within the population brought on by environmental variability than the ability for managers to impose mortality rates via removal efforts. Thus, management actions can be more effective if plans are implemented to more strongly compound mortality already imposed by the environment.

Carp control is often a management focus because the carp are easily identifiable, impacts on the aquatic ecosystem are well documented, and solutions for decreasing their impacts are intuitive (i.e. reduce or eradicate the species; Weber & Brown, 2009). However our modeling results demonstrated that wind resuspension is one of the main drivers of suspended sediment concentrations (SSC), and thus also adds to the currently turbid state of Malheur Lake. Furthermore, the level of SSC in Malheur Lake at any time is driven by both physical and environmental factors (i.e. water depth, wind fetch, and wind speed), and therefore, management actions targeted at reducing the deleterious effects of wind and wave resuspension

(i.e. wave reduction barriers) could be used to decrease the overall SSC and thus increase the light in the water column. Collectively the results from this thesis reinforce the notion that future restoration actions in Malheur Lake must be more broadly focused (i.e. systems perspective) and allow the alternative stable states theory to guide future management decisions (Scheffer et al., 1993; Janssen et al., 2014; Williams, 2005).

Based on the alternative stable states theory, shallow lakes can exist in a clear or turbid state, and these states are driven and maintained by reinforcing (positive) feedback loops that pull the system towards one of the two states (Scheffer et al., 1993; Janssen et al., 2014; Williams, 2005). While there are numerous auxiliary factors that collectively add energy to the reinforcing feedback loops, the presence and or absence of aquatic macrophytes is the main driver that stabilizes either of these states in perpetuity. For instance, aquatic macrophytes reduce wind driven sediment resuspension via shortening the effective wind fetch and securing the sediment which subsequently reduces internal phosphorous loading and promotes the establishment of benthic algae (Horppila et al., 2013; Zhang et al., 2013). The establishment of benthic algae further removes nutrients from the water column and decreases the susceptibility of the sediment to wind resuspension. (Zhang et al., 2013). Furthermore, aquatic macrophytes provide structural habitat for zooplankton, thus increasing their negative effect (predation) on the phytoplankton biomass, which further increases the water clarity (Timms & Moss, 1984). Lastly, aquatic macrophytes use nutrients available in the water column, can release allelopathic chemicals, and oxidize the sediment, all of which decrease the amount of phosphorous available to phytoplankton, thus further reducing the phytoplankton biomass (Wium-Andersen et al., 1982; Carpenter et al., 1983; Ozimek et al., 1993; Williams, 2005). However, in the context of restoration, aquatic macrophytes are generally only described for their benefit as habitat to residential and migratory bird species (i.e. material, food, shelter,

etc.), and not as a system stabilizing mechanism that is crucial to the maintenance of the clear state.

Due to the importance of macrophytes to initiating and maintaining the clear state, monitoring of the effectiveness of future restoration projects would benefit by tracking effects of management actions on the establishment and growth of macrophytes (emergent/submergent). For instance, a carp project aimed at reducing carp biomass to a certain threshold (i.e. kg/ha) could first demonstrate how a reduction in carp biomass below a desired threshold will clear the water column and ensure the establishment and growth of macrophytes in perpetuity (i.e. Is transplanting aquatic vegetation necessary? Will a reduction in carp biomass promote increased macrophyte seed germination? Will both emergent and submergent vegetation benefit?). Furthermore, future lake restoration projects could benefit by establishing a goal of increasing water clarity such that a minimum level of incoming photosynthetic active radiation reaches the sediment during the spring months (e.g., a 3% hypothesized threshold to promote macrophyte growth; Istvánovics et al., 2008; Wersal et al., 2006).

To eventually overcome the momentum of the reinforcing feedback loops pulling Malheur Lake towards the turbid state, results of this research indicate that a large perturbation is likely needed. Therefore, the scenarios that I have modeled here individually will likely in themselves be ineffective at shifting the lake back to the clear state because their forces are too small in the context of Malheur Lake; therefore, a more large-scale transformative effort may be necessary to not only flip the current state, but also maintain the clear state in perpetuity (Williams, 2005; Kates et al., 2012). For instance, a large-scale hydrologic manipulation in the form of lake subdivision (carp management, wind fetch reduction, water manipulation) may be successful at initiating the reinforcing feedback loops and flipping the system to the clear state (Griffiths, 1978). However, such a large transformative effort would entail a significant pulse



of investment and infrastructure, which would likely require substantial buy-in from collaborators and stakeholders involved with restoration (Kates et al., 2012). Therefore, future restoration efforts in Malheur Lake will likely require explicitly working within a socio-ecological dynamic to guide future restoration actions that are successful in both dimensions.

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## Appendix A: CarpMOD - Population Dynamics Model Equations and Parameters

### State Variable Equations

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

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

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

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

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

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

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

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

### 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:

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

where  $L_{(A)}$  is the length (mm) of the carp at age,  $L_{\infty}$  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, 2017a/b).

### 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, 2017a). 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, 2017a).

### 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,

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

where  $\rho_i$  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  $\pm$  31.754 and LM95 = 364.667  $\pm$  47.343 mm; Brown & Walker, 2004; Brown & 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 & 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,  $\alpha$  is the coefficient that is density-independent, and  $\beta$  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  $\alpha$  and  $\beta$  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 & Walker, 2004; Brown & 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:

$$V_{(A)} = 1 - e^{-0.06\left(\frac{L_{(A)}}{L_{\infty}}\right)^{-1.5}} + 10^{-4} \cdot D$$

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  $L_{\infty}$  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.

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

Model component	Equation	Reference
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	$\rho_i = (1 + e^{\ln((19)(L_{(A)} - LM50)/(LM50 - LM95))})^{-1}$	Brown & Walker, 2004
Ricker Recruitment	$R = a * S * \exp(-\beta * S)$	Ricker, 1954; Brown & Walker, 2004
Annual Natural Mortality	$V_{(A)} = 1 - e^{-0.06\left(\frac{L_{(A)}}{L_{\infty}}\right)^{-1.5}} + 10^{-4} \cdot D$	Charnov et al., 2013; Bajer et al., 2015

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

Parameters	Symbol	Function	Mean	Variance	Reference
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.	$L_{\infty}$	VBGM	818.02754	41.3931	Derived via data from Malheur Lake
Alpha Coefficient	$\alpha$	Recruitment	20.0825	16.1242	Brown & Walker, 2004; Brown & Gilligan, 2014
Beta Coefficient	$\beta$	Recruitment	0.0162	0.0039	Brown & Walker, 2004; Brown & Gilligan, 2014
Len. of Maturity 50	LM50	Maturity	309.667	31.754	Brown & Walker, 2004; Brown & Gilligan, 2014
Len. of Maturity 95	LM95	Maturity	364.667	47.343	Brown & Walker, 2004; Brown & Gilligan, 2014

## Appendix B: 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 & 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, 2013-2015); where data were not available from Malheur Lake, values were derived from the literature (Table 1).

Table B.1. Parameters used as inputs into the avian bioenergetics for the three avian piscivores (Double-crested Cormorant, American White Pelican, and Caspian Tern).

Parameters	Units	Tern	Cormorant	Pelican	Reference
Average Body Mass	g	650	2275	7000	Evans & Knopf 1993; Lyons 2010
Field Metabolic Rate	kJ/d	11.49m <sup>0.718</sup>	11.49m <sup>0.718</sup>	3.90m <sup>0.87</sup>	Ellis & Gabrielsen, 2001
Assimilation Efficiencies		0.75	0.75	0.75	Brugger 1993; Miller & Reinecke, 1984; Lyons & 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

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, 2013-2015). 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 2013-2015). We translated the lengths of carp consumed into biomass of carp consumed using a previously documented weight-length relationship (Schneider et al., 2000), which 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).

### **Appendix C: Basic Hydrologic Model**

Lake area was best predicted by: 1) the intercept (mean  $\pm$  SE;  $3435.25 \pm 8809.56$ ); 2) previous year's lake area (ha; FA\_LA\_M1;  $0.77 \pm 0.05$ ), 3) discharge (cms; water year; WY\_BLITZ\_CMS;  $16.21 \pm 1.22$ ) from the Blitzen River, and 4) date of 50% total discharge (Julian date; WY\_BLITZ\_DAY\_50\_DIS;  $-163.89 \pm 71.26$ ) from the Blitzen River ( $F(3,32) = 193.9$ ;  $R^2 = 0.948$ ; Adjusted  $R^2 = 0.943$ ; Residual Standard Error = 3663). The future stochastic lake area fluctuation scenarios were simulated by randomly selecting model parameter values (WY\_BLITZ\_CMS and WY\_BLITZ\_DAY\_50\_DIS) from a normal distribution based on the mean and standard deviation, which were compiled via 107 years of Blitzen River discharge data.

Table C.1. Comparison of the Global and Final Model outputs from the multiple linear regression using the stepwise model selection procedure (see Methods).

Parameters	Units	Model Input Name	Global Model	Final Model
		Intercept	-2804.00	3381.98
Fall Lake Area (Previous Year)	ha	FA_LA_M1	0.80 ***	0.77 ***
Fish Creek Total Snow Accumulation	cm	FC_CM_MAX	-14.36	
Fish Creek SWE	cm	FC_SWE_MAX	-13.31	
Star Ridge Total Snow Accumulation	cm	SR_CM_MAX	109.00	
Star Ridge SWE	cm	SR_SWE_MAX	139.50	
Degree Day Temps (Water Year)	C	WY_TEMP_C	1.86	
Degree Day Temps (Summer Months)	C	JJAS_TEMP_C	-4.71	
Blitzen River Discharge	cms	WY_BLITZ_CMS	14.10 ***	16.21 ***
Blitzen River 50% Discharge	day	WY_BLITZ_DAY_50_DIS	-112.50	-163.60 *
Degrees of Freedom (DF)			26	32
Number of Parameters (K)			9	3
Multiple R-Squared ( $R^2$ )			0.9522	0.9479
Adjusted R-Squared ( $R^2$ )			0.9357	0.9430
F-Statistic			57.57	193.9