MODELING POPULATION AND DISEASE DYNAMICS OF GREAT LAKES FISH EXPOSED TO PFAS

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife—Master of Science

2025

ABSTRACT

Per- and polyfluoroalkyl substances, otherwise known as PFAS, chemicals have been produced since the 1940s and are suspected to be harmful to humans, wildlife, and the environment. Previous research has found these compounds to have toxic effects on lipid metabolism, hepatotoxicity, immunotoxicity, development, reproduction, and growth in humans and various aquatic species. These compounds have been found in all five of the Laurentian Great lakes as well as within many of the valuable fish species that reside in the lakes. I created simulation models to explore population-levels effects on species such lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*) and steelhead (*Oncorhynchus mykiss*) populations stemming from PFAS contamination effects on factors such as fish growth, fecundity, disease mortality, and egg survival. For interactions with disease, I used an infectious disease model that simulated lake whitefish exposures to viral hemorrhagic septicemia virus (VHSV), lake trout exposures to epizootic epitheliotropic disease virus (EEDV), and steelhead exposures to *Flavobacterium psychrophilum.* The population model results showed that decreases in growth in terms of weight and relative fecundity (i.e., eggs per kg) had the largest effect on population abundances across all three species. When factors were modeled in combination, all three species were predicted to experience 80% declines in abundance over a 65-year period. The results of the disease transmission model found that PFAS exposure caused the largest percentage increase in the maximum proportion of infected steelhead.

ACKNOWLEDGMENTS

First, I would like to thank my advisor and mentor, Cheryl Murphy, for all the support you have given me over the last two and a half years. You have taught me so much, not only about PFAS, but about how to create a positive work environment where every team member feels valued and important. The knowledge you have shared with me throughout my graduate studies will no doubt help me in all my future scientific endeavors, and I am very thankful that you were able to be my advisor.

I would also like to thank the other two members of my graduate committee, Travis Brenden and Jean Tsao. You have both been so understanding and supportive throughout the last couple of years, and your knowledge and experience have been incredibly helpful for my research. In addition, I would like to thank all the members of the Murphy lab that I have been able to work with, Adrian Deil Manliclic, Rachel Leads, Allie Sexton, Lori Ivan, Koji Sano and Mason Laney. You have all helped to create such a positive learning environment, and I have learned so much from each one of you. I also want to thank and acknowledge Sara Iverson and Chris Vandergoot for connecting me to the Quantitative Fisheries Center at Michigan State University.

A special thanks goes out to everyone who has helped to provide me with fisheries data to use in my models, including Travis Brenden, Ben Turshak, Steve Lenart, and Richard Clark. I would also like to acknowledge everyone I have had the privilege of working with in both the Center for PFAS Research and the Quantitative Fisheries Center. You have all been a joy to get to know and I have learned a lot from the work that you do and the passion you have for science. In addition, I would like to thank the Great Lakes Fisheries Trust and the Quantitative Fisheries Center for providing the funding for conducting this research.

Finally, I would like to thank my closest friends and family for providing support and encouragement in both the good and bad times throughout the last couple of years. You have all helped to keep me on track and help me to work through the tough times that graduate school has thrown at me. A special thank you goes out to my mom, Jenny, for always answering my phone calls even though you knew it would be a rant about random PFAS facts, me convincing you to test our well water at home or just letting you know I was stressed and that I needed to talk to my mom. You always encouraged me to never give up and that I could do anything I put my mind to.

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INTRODUCTION

Per- and polyfluoroalkyl substances, otherwise known as PFAS, have been produced since the late 1940s and are gaining increased attention because of the widespread occurrence and associated health concerns in both humans and wildlife. These chemicals comprise long carbon chains with fluorine atoms attached and have both hydrophobic and lipophobic properties (McCarthy et al., 2017). The properties of these chemicals and the strength of the bond between carbon and fluorine make them economical and effective, and as such, these chemicals are commonly used in several products, including, Teflon, fire-fighting foams, food packaging, surface protecting agents, and lubricants (Denys et al., 2014). Although these attributes of PFAS are useful for commercial and mass-produced products, their inability to break down leads to environmental persistence.

PFAS chemicals enter the environment via multiple pathways, including, air emissions, landfill leachate, aqueous film-forming foam (AFFF), and wastewater disposal. After entering the environment, the chemicals often mobilize and travel between soil, sediment, surface water, ground water, air and rain. As of March 2021, there were over 2,330 reported ground or drinking water contamination sites throughout the United States (Renfrew and Pearson, 2021). The EPA's Fifth Unregulated Contaminant Monitoring Rule (UCMR-5) requires PFAS drinking water tests to be reported when detection levels exceed 4 parts per trillion (ppt). As of November 2024, the UCMR-5 data identified 2,394 sites across the United States with levels above this limit (Environmental Working Group, 2024). Groundwater contamination can create a long-term issues as the PFAS are eventually transported to drinking, surface and rain water. It is estimated that 32 ± 7 kg/ year of PFAS was discharged from a contaminated groundwater source into five tributaries, which were feeder streams for the Cape Fear River (Pétré, 2021). The transport of these chemicals poses a serious threat to wildlife health as they bioaccumulate and cause health risks. The ability of PFAS chemicals to easily be transported via water over large distances, without degrading, causes potential environmental harm beyond the initial entry to the environment.

Giesy and Kannan (2001) were the first to examine the global distribution of PFAS chemicals in wildlife and found widespread contamination of perfluorooctanesulfonic acid (PFOS) with urban areas having a much greater concentration of PFOS than rural areas. In 2005, Kannan et al. (2005) found that PFAS concentrations in the benthic food web of the Great Lakes were 1000-fold greater than those in the surrounding water. They also found that predatory fish had concentrations that were 10-20 fold greater than the concentrations in prey fish (Kannan et al., 2005). This study suggested that PFAS compounds may bioaccumulate in species that are in higher trophic levels on the food chain. In more recent years, similar trends show that PFOS was dominant in aquatic species and the highest levels were found in smallmouth bass; a known top benthopelagic predator (Munoz et al., 2022). Since the release of the early 2000s studies, there has been a rapid increase in research on PFAS chemicals, their distribution and their toxicological effects in efforts to understand the risk to humans, fish and wildlife.

As a result of the widespread use of PFAS, these compounds can be found at high concentrations in many biological organisms. For aquatic species, PFAS dissolves easily into freshwater and marine systems, and can be taken up through ingestion or respiration (Illinois Department of Public Health, 2024). Although there is contamination in both the marine and freshwater ecosystems, several studies have shown that freshwater fish have higher concentrations of PFAS than marine species (Denys et al., 2014).

Studies have found that bioaccumulation factors (BAFs) are larger for longer-chain PFAS chemicals relative to shorter-chain (Pan et al., 2014). This bioaccumulation pattern suggests that wildlife exposed to contaminated water bodies over long periods of time may accumulate these compounds and biomagnify them in the food chain.

The Laurentian Great Lakes of North America, which contains approximately 20% of the world's freshwater, have become contaminated with PFAS chemicals (Alwin et al., 2024). The Great Lakes is the drinking water source for more than 30 million people, which accounts for 10 percent of the US population and 30 percent of the Canadian population (EPA, 2025). The Great Lakes are also home to many valuable fisheries that have served as a major food source for the area for millennia. (Ebener et al., 2008). Some of the most important species, in terms of valued fisheries and the fish populations that support these fisheries, include lake trout, walleye, lake whitefish, white bass, yellow perch and prey species like alewife, ciscoes, shiners and gizzard shad (Great Lakes Fisheries Commission, 2021). Contamination of the Great Lakes with PFAS chemicals is concerning for the health of humans consuming resources from this region, along with other biological organisms who rely on these lakes for their habitat.

The major toxic effects of PFAS contamination for both humans and wildlife are demonstrated disruptions in lipid metabolism, hepatotoxicity, immunotoxicity, hormonal and developmental effects (Pan et al., 2014). The ability for PFAS exposure to weaken immune responses within organisms is a cause for concern in the Great Lakes because there are several pathogens that threaten vulnerable fish populations in this region. PFAS contaminated fish populations may have weakened immune responses, which could impact how the pathogen spreads and ultimately affects the fishery's population.

Despite the potential effects these chemicals may have on Great Lakes fish, there have been little to no efforts to incorporate the toxic effects of PFAS into population level models. The main factors that influence population abundance are mortality, growth and recruitment, all three of which may be affected by PFAS exposure (Allen and Hightower, 2010). Exposure to PFAS can also lead to the down regulation of specific genes and receptors that can harm immune function and inflammatory reactions, both of which may play a part in the susceptibility and spread of pathogens throughout impacted fish populations (Zhang et al., 2020). To bridge the gap between toxicological research in this field with population and pathogen infection dynamics occurring in fish living in the Great Lakes watershed, I created two separate simulation models; one that simulates PFAS's impact on population dynamics and one that simulates the spread of pathogens throughout fish populations.

STUDY OBJECTIVES

The aim of this thesis was to study the toxicological effects of PFAS contamination in freshwater fish and how these effects may lead to declines in fish population abundance. This work sheds light on the potential effect of PFAS contamination on the spread of infectious pathogens in fish populations. The overarching objectives of this study were to 1) incorporate current research about reproductive, developmental, and immune effects of PFAS into a population model to investigate the impact of individual effects on the population abundance of fish and 2) determine model parameter sensitivity and identify how PFAS may impact these parameters.

The first chapter of this thesis presents an age-structured population model that simulates population abundance when some of the population is exposed to PFAS. This model incorporates PFAS effects on fecundity, egg survival, growth, and disease mortality on population abundance and spawning stock biomass. For the second chapter, three specific pathogens that are stressors to Great Lakes Fish were investigated; these include, *Flavobacterium psychrophilum*, causative agent of bacterial coldwater disease (Loch and Faisal 2017), epizootic epitheliotropic disease virus (EEDV), which is a large contributor to lake trout mortality in hatcheries, and viral haemorrhagic septicaemia virus (VHSV), which has led to mortality events in several species throughout the Great Lakes (Faisal et al., 2019; Groocock et al., 2007). An SIR model was constructed to show how the proportion of susceptible (S), infected (I) and recovered (R) fish vary throughout the course of a year and each model was parameterized specifically to each fish species and the pathogen threatening their population. The final chapter captures the main conclusions from both modeling chapters and dives into the questions concerning this topic that should be addressed in the future.

CHAPTER 1: POPULATION DYNAMICS OF LAKE TROUT (*SALVELINUS NAMAYCUSH*), LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) AND STEELHEAD TROUT (*ONCORHYNCHUS MYKISS*) EXPOSED TO PFAS

1. INTRODUCTION

The Laurentian Great Lakes contain 20% of the planet's freshwater, providing drinking water for an estimated 35 million people and important habitat for numerous economically and ecologically important fish populations (Morton, 2021). The total economic value from recreational and commercial fisheries in the Great Lakes has been estimated at approximately $5.1 billion dollars annually with the fishing industry supporting over 75,000 jobs (GLFC, 2024). These lakes have also been a home and provider of natural resources for Native American tribes and bands for thousands of years along with providing a route of transportation by canoe (Davis & Ensign, n.d.). Some of the important fisheries in this region include steelhead, *Oncorhynchus mykiss*, lake whitefish, *Coregonus clupeaformis*, and lake trout, *Salvelinus namaycush.* Lake trout are a native species to this region and are important for both commercial and sport fisheries, however their populations have been threatened from predation by sea lampreys (Lantry et al., 2015). Lake whitefish are an important commercial fish from the Great Lakes region and they play an important role in the ecosystem as both a food source and consumer of small fish, zooplankton and other bottom dwelling invertebrates. They have also been used as a food source for inhabitants of this geographical area for thousands of years (Ebener et al., 2008). Steelheads (i.e., migratory form of rainbow trout) are also a key species in this region although they are not native to this area, they were introduced to the Great Lakes from the Pacific coast (Willoughby et al., 2018). The life history traits and population levels of these species are diverse, with notable differences in fecundity, the status of each population, the number of spawning events that occur throughout their lifecycle and how long each species typically lives for (Table 1.1).

Table 1.1 Major life history characteristics and traits for lake whitefish, lake trout and steelhead trout. Fecundity values are estimated for fish at time of spawning.

Species	Location	Reproduction	Spawning Time	Spawning Location	Adult Diet	Age	Size	Fecundity	Other	Sources
Lake Whitefish *(Coregonus clupeaformis)*	Benthic, cool water fish.	Iteroparous, broadcast spawners and no parental involvement.	Typically spawn in November and December.	Spawning occurs in shallow waters.	Zooplankton, small fish and fish eggs.	Lake whitefish typically live to 20-30 years old.	Typically between 17-22 inches and weigh between 0.68-1.81 Kg.	An individual female can lay between 10,000 and 130,000 eggs.	Populations have been declining for last 50 years or so.	Michigan Sea Grant (2025), *Lake Whitefish;* Negro (2025); Maine Department of Inland Fisheries and Wildlife (2024).
Lake Trout *(Salvelinus namaycush)*	Often found in cool, deep water. Can also be found in relatively shallow water outside of the summer months.	Iteroparous, broadcast spawners and no parental involvement	They spawn during the fall months, typically October through November.	Spawning takes place in shoals or shallow reefs and they return yearly to same spawning area.	Feed primarily on other fish, sometimes crustaceans, plankton and insects.	Lake trout often live to be 20+ years old.	Average adult weighs 4-4.5 Kg with lengths between 24-36 inches.	Single female may lay between 2,000 to 20,000 eggs depending on size.	Commercial fishing and sea lamprey greatly reduced populations in the 1900s but stocks appear to be coming back.	Michigan Department of Natural Resources (n.d.), *Lake Trout;* U.S. Fish and Wildlife Service (n.d.).
Steelhead Trout	Adults in the lake dwelling potion of life are typically found in water less than 35 feet deep and can be found near stream outlets in spring and summer prior to spawning.	Iteroparous and spawn into nests called redds. These redds are 4-12 inches deep and are covered with gravel after male fertilization.	In the Great Lakes region, steelhead enter their spawning streams between late October and early May with most spawning occurring in spring.	After 1-4 growing seasons in the lake, they return to a freshwater stream to spawn.	Adults primarily eat small fish, crustaceans, mollusks and insects.	Steelhead usually survive between 6-8 years in the Great Lakes region.	Typically 16-36 inches and weigh 4-5 Kg, with some weighing up to 9 Kg.	Females lay between 200 to 8,000 eggs that are deposited in a redd. They may spawn annually or skip years in between spawning.	Young steelhead, called parr, spend the first 1-3 years of life in their home stream before migrating to a lake. Larger, older, female steelhead survive spawning at higher rates and 20-30% of steelhead return to spawn for a second time.	Michigan Sea Grant (2025), *Searching for Steelhead;* Alaska Department of Fish and Game (n.d.).

The Great Lakes ecosystem have been subject to numerous perturbations including establishment of invasive species that detrimentally affect native species because of competition for habitat and food resources, elevated levels of predation because of the resurgence of wild reproduction, spread of harmful pathogens, elevated water temperatures and lower ice coverage during the winter months because of rising water temperatures, and elevated point and non-point source pollution (Alwin et al., 2024). All of these threats can impact population persistence of native species within the Great Lakes region. Notably, since 2015, the lake levels in the Great Lakes region have fluctuated more widely because of variable rainfall stemming from climate change. Rising lake levels have caused impacts on homes, flooding, erosion and various shoreline infrastructures. These high volumes of water also bring increased levels of pollutants into this system such as nitrogen, phosphorus, *E. coli* and toxic contaminants like per- and polyfluoroalkyl substances (PFAS) (Morton, 2021; Xia, 2024).

Monitoring precipitation studies, that used passive air samplers to monitor atmospheric deposition and taking water samples from the lakes suggests that Lake Michigan, Lake Superior and Lake Huron tend to accumulate PFAS over time, while Lake Ontario and Lake Erie can eliminate the compounds or remain at a steady state of contamination (Xia et al., 2024). These sampling results were then used in calculations aiming to identify the net mass transfer flows of PFAS in the lakes. Although two of the Great Lakes had a positive net mass transfer flow, and gradually eliminated the PFAS via outflow and sedimentation, these compounds were still present in the various samples taken in this experiment and have the potential to impact local wildlife as they cycle between different water bodies and accumulate in sediments and prey organisms (Xia et al., 2024).

The effects of PFAS on humans, animals, fish, and wildlife is of concern because these compounds can cause adverse effects on organism-level reproduction, growth, and development, as well as sub-organismal and molecular impacts on genes and receptors related to liver and immune function. For example, chronic exposure of Zebrafish (*Danio rerio)* to perfluorooctanoic acid (PFOA), a well-studied 8-carbon chain PFAS variant, reduced the percentage of viable embryos, lowered body weight and length, changed gene expression, decreased fecundity and slowed development from embryo to free swimming larval stages (Jantzen et al., 2017). Additionally, acute exposure of zebrafish to perfluorooctane sulfonate (PFOS), resulted in a 34% reduction in fecundity relative to the control group after being exposed to 0.5 mg/L of PFOS for two weeks; after 3 weeks of exposure, there was a 47% reduction in fecundity (Sharpe et al., 2010). The effects of PFAS contamination may pose a serious threat to Great Lake's fisheries causing population level effects due to changes in growth, reproduction, mortality, and recruitment (Allen and Hightower, 2010).

To date, there has been limited population-level evaluation of PFAS contamination effects. Given the effects of PFAS on fecundity, weight, length, egg survival and development, this chapter aims to incorporate these toxic effects into a Leslie matrix model to simulate the potential population level effects. I constructed an age structured, discrete population model that allows the incorporation of PFAS effects into the fecundity and survival probabilities. This modeling framework allows for these specific effects, along with any new effects that are discovered in coming years, to be incorporated so that we can explore impacts of PFAS exposures on populations. The three key fisheries, lake trout, lake whitefish and steelhead, will be used as the model species in this chapter as their populations already face several challenges. The objectives of this chapter are to 1) investigate the impact that sublethal PFAS effects can have on the population abundance, 2) identify which specific PFAS effects have the largest impact on the population abundance, 3) pinpoint which model parameters have the largest effect on the average total population abundance, and 4) explore which species seem to be impacted the most from these sublethal effects, based on life history demographics.

2. METHODS

2.1. STUDY AREA

Lake Michigan is the 2nd largest Great Lake by volume and supports 179 different fish species, including several important, historic, commercial fisheries such as lake whitefish, lake trout and cisco (Global Great Lakes, n.d.). The lake has an average depth of 279 feet (85 meters) and a maximum depth of 923 feet (281 meters), Management of lake whitefish and lake trout populations across large areas of Lake Michigan is a cooperative process between the state of Michigan, several Native American tribes and the US Fish and Wildlife Service stemming from the 1836 Treaty of Washington that ceded 16 million acres of land to the U.S. government. As a result of the 1836 Treaty, Lake Michigan and Huron are divided into 18 different management units for lake whitefish, 8 of which are in Lake Michigan's waters (Figure 1.1; Deroba and Bence, 2012). For lake trout, Lake Michigan is split up into 8 management units within the 1836 Treaty Waters (Figure 1.2). These individual management units have specific data for each of the populations present in each geographical location.

Lake Michigan is an oligotrophic lake and has faced several environmental stressors from nutrient runoff to invasive species to PFAS contamination. Major sources of PFAS contamination include industrial sources, wastewater treatment plants, military bases and airports using firefighting foams (Miranda et al., 2023).

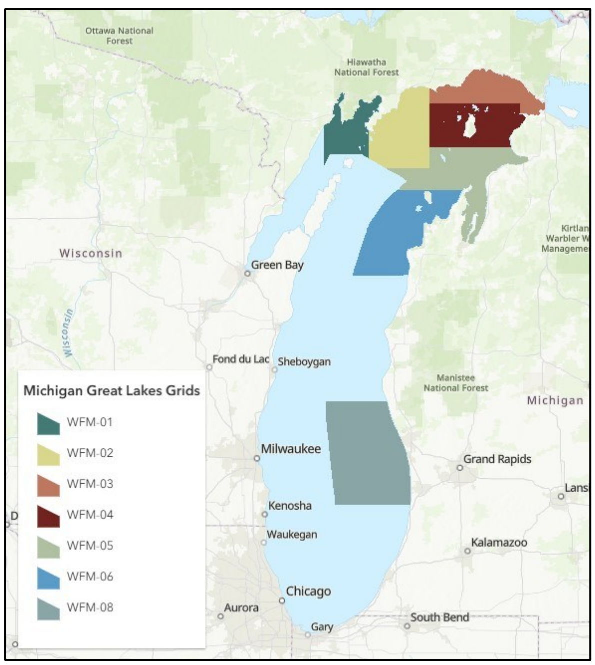

Figure 1.1 Lake whitefish commercial management units in Lake Michigan. For this model, only units 1,2,3,4,5,6, and 8 were incorporated into the model.

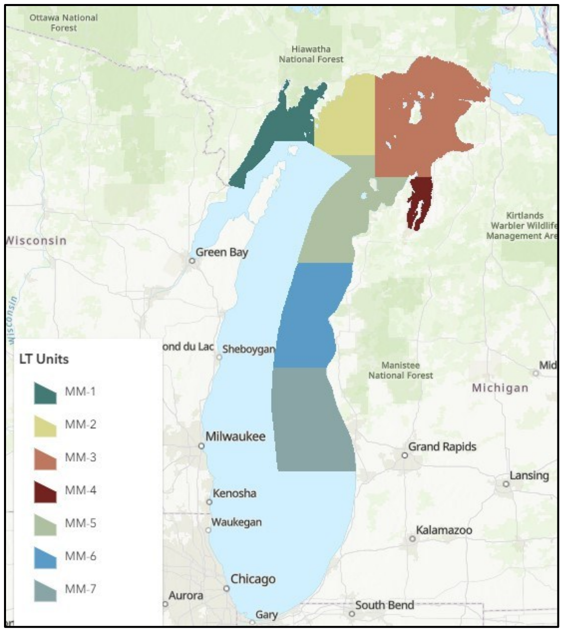

Figure 1.2 Lake trout commercial management units in Lake Michigan. For this model only units 1,2,3,4,5,6 and 7 were modeled.

2.2. MODEL DESCRIPTION

A Leslie matrix model was used to simulate population abundances for lake trout, lake whitefish and steelhead. This model simulated annual age-specific population abundances by multiplying a vector of initial population abundances by the Leslie Matrix (Figure 1.3; Eq. T1.2.1). A full list of the parameters and symbols used in this model can be found in Table 1.3. The first row of the matrix contained age specific fecundity values (eggs per female), while the subsequent rows consisted of survival probabilities from age class a to a+1. Abundances were projected over a duration of 65 years; however, the first 15 years were excluded from analysis to allow the population to reach dynamic equilibrium. The outputs of the model were age specific population abundance per year, births per year and total population abundance per year.

Table 1.2 Equations used in the population model. Equation T1.2.1 is the general equation for Leslie matrix multiplication and T1.2.5 represents the multiplication occurring for each age class to reach age a+1.

Equations	
$N_{t+1} = L \times N_t$	(T1.2.1)
$SSB_a = N_a m_a W_a P_f E$	(T1.2.2)
$u = \frac{F}{Z}(1 - e^{-Z})$	(T1.2.3)
$v = \frac{M}{Z}(1 - e^{-Z})$	(T1.2.4)
$N_a s_a = N_{a+1}$	(T1.2.5)
$R_t = \alpha S_t e^{-\beta St}$	(T1.2.6)
$\ln\left(\frac{R_t}{St}\right) = \ln(\alpha) - \beta S_t$	(T1.2.7)
$\alpha = e^{\left(\ln(\alpha) + \frac{\sigma^2}{2}\right)}$	(T1.2.8)
$cv = \frac{\sigma}{\mu(mean)}$	(T1.2.9)

Table 1.3 Descriptions of symbols, parameters and variables used in the population model.

Symbol	Description
a	Age
t	Time (in years)
L	Leslie Matrix
SSB	Spawning Stock Biomass (measured in number of eggs)
m	Maturity (proportion of mature fish)
W	Weight (kg)
P_f	Proportion of females
E	Eggs/ kg of fish
u	Discrete fishing mortality
v	Discrete natural mortality
F	Instantaneous fishing mortality
M	Instantaneous natural mortality
Z	Instantanoues Total Mortality
s	Survival probability
α	Ricker density independent parameter
β	Ricker density dependent parameter
R	Number of recruits
S	Number of spawners
σ	Standard deviation
cv	Coefficient of variation
μ(mean)	Mean
N	Population abundance
σ^2	Residual square error

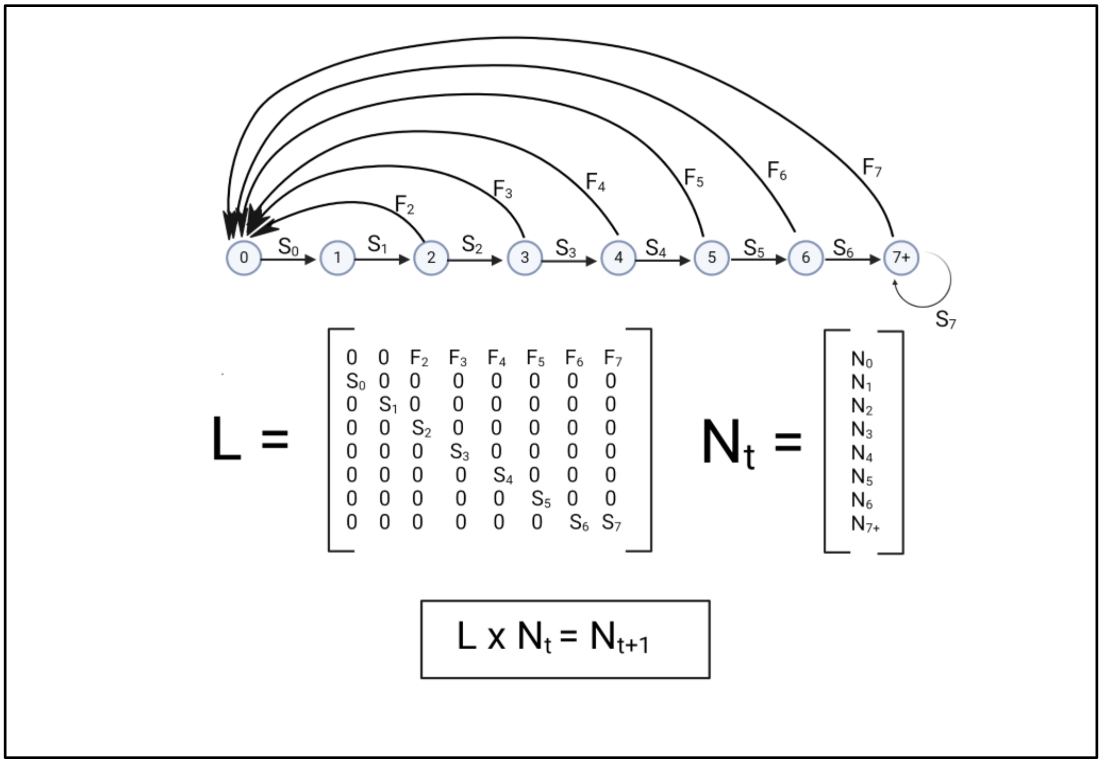

Figure 1.3 Basic Leslie matrix model structure with 7 age classes. N_t is the population abundance at time t and N_i (i = [0,1,2,3,4,5,6,7]) is equal to the abundance for each specific age class. L is representative of the Leslie Matrix used for modeling. Created with BioRender.com.

To incorporate PFAS exposure into the model, a parameter named "percent_pfas" was included to divide up the total population (sum of all age classes) into two groups, one being a proportion of the population that was considered exposed to PFAS and the other being the control group that was not exposed to PFAS. The proportion of fish that were considered exposed to PFAS used an alternate Leslie Matrix with either singly imposed differences in their fecundity, egg survival, weight at age, disease mortality or a combination of all these effects. At the start of each yearly time step, the total abundance of fish was multiplied by this "percent_pfas" parameter to ensure that the designated percentage of fish would be exposed each year. This PFAS exposed portion of the population was consistent across all age classes and years that the model was run.

The data for all three species that were used to inform the baseline matrix model were from Michigan DNR fishery monitoring data and statistical catch at age models (SCAA models) (Newman et al., 2021; Turschak et al., 2021; Lenart, 2024). These datasets included abundances at each age, weight at age, spawning stock biomass, proportion of females, eggs per kg, egg abundances, and rates of maturity, along with fishing and natural mortality rates. One main assumption of this model is that the data from wild fish stocks are representative of the control population which are not considered to be exposed to PFAS. I made this assumption because PFAS has been manufactured since the 1940s and it is likely that the fish in the Great Lakes region have already been exposed to PFAS to varying extents, but without knowing the full extent of the contamination, I opted to assume baseline conditions meant no exposure. Given the structure of lake trout and lake whitefish management units, each individual unit was modeled separately, assuming that each unit was an isolated population, to best represent the specific dynamics occurring in each geographical region (Figures 1.1, 1.2). The output data from these different units were combined to show the dynamics occurring in Lake Michigan as a whole, however, there were no datasets available for lake trout unit MM-8 or lake whitefish unit WFM-07 (Figure 1.2) so these management units were not modeled and do not make up the Lake Michigan total population results. The dataset for steelhead trout was representative of the entire Lake Michigan region, therefore, this species had one model that reflected the dynamics of the whole population.

2.3. REPRODUCTION

Reproduction was estimated using maturity, eggs per kg of fish, weight at age, and proportion of female fish data. Age specific relative fecundity levels were calculated as the number of eggs per kg of fish that females were expected to produce (Deroba and Bence, 2012;

Eq. T1.2.2). The eggs/kg values were specific to each species but were assumed to be constant across all management units for lake trout and lake whitefish. When these age specific fecundity values in the Leslie matrix were multiplied by the population abundance vector, the total number of eggs produced across all ages were represented as the age 0 abundance for the next yearly timestep. All parameter values for weight at age and maturity at age for each specific species and management unit can be found in the Appendix Tables A1.12-A1.23.

Lake Whitefish

The proportion of mature fish at each age, weight at age and proportion of female fish came from the MDNR datasets and were specific to each management unit (Table 1.4). The number of eggs/kg came from fisheries data (19000 eggs/kg, Ebener et al., 2021). The weight at age data was defined specifically as the weight per fish at the time of spawning and was given in kilograms.

Lake Trout

The lake trout dataset did not include information about the proportion of females in the population, so it was assumed to be 50% (Table 1.4; Appendix, Tables A1.12-A1.23). This came from an assumption made in the stock assessment data that there was a 1:1 ratio of males to females (Lenart, 2024). The fisheries data for lake trout showed females laying 1508 eggs/kg (Table 1.4, Lenart, 2024). The lake trout datasets did not include spawning weight at age, so for this species, the weight at age was not specific to the time of spawning and was just representative of the average weight per age class.

Steelhead

Available steelhead data did not include the proportion of females in the population, so this was also assumed to be 50% (Table 1.4; Appendix, Tables A1.12-A1.23). The eggs/kg value came from an estimate of 3740 eggs per female with the average spawning steelhead weighing 3.2814 kg, when the average number of eggs was divided by the weight, it resulted in 1139.75 eggs/kg (Table 1.4, Ward and Slaney, 1988).

Table 1.4 Non-age specific parameter values for lake whitefish, lake trout and steelhead trout. These parameters are used for fecundity estimates, ricker modeling to show density dependence, stochasticity and survival probabilities.

Species	Management Unit	Control Eggs/Kg	Proportion Female	Ricker Alpha	Ricker Beta	Target Coefficient of Variation	Control Disease Mortality	Egg Survival
Lake Whitefish	WFM-01	19000	0.51	0.693	-1.3E-07	0.236766543	0.02964	1.81E-04
Lake Whitefish	WFM-02	19000	0.48569	0.9094	-6.42E-07	0.236766543	0.02964	1.13E-04
Lake Whitefish	WFM-03	19000	0.4818	0.79357	-3.01E-07	0.236766543	0.02964	3.47E-04
Lake Whitefish	WFM-04	19000	0.483	1.40412	-9.43E-07	0.236766543	0.02964	8.41E-05
Lake Whitefish	WFM-05	19000	0.45	1.89751	-3.21E-06	0.236766543	0.02964	8.65E-05
Lake Whitefish	WFM-06	19000	0.517	0.63753	-3.07E-06	0.236766543	0.02964	9.37E-05
Lake Whitefish	WFM-08	19000	0.507	0.8278	-3.25E-07	0.236766543	0.02964	7.89E-05
Lake Trout	MM-123	1508	0.5	1.29305	-1.74E-06	0.261225	0.03612	2.95E-03
Lake Trout	MM-4	1508	0.5	1.21245	-4.13E-06	0.247206987	0.03612	2.64E-03
Lake Trout	MM-5	1508	0.5	0.9889	-9.04E-06	0.239084757	0.03612	3.38E-03
Lake Trout	MM-67	1508	0.5	2.85586	-8.65E-06	0.249009502	0.03612	1.55E-03
Steelhead Trout	Lake Michigan	1139.75	0.5	1.18044	-1.07E-06	0.177452	0.0504	2.34E-04

2.4. SURVIVAL

Age-specific survival rates were determined by summing exploitation rate and fraction of fish expected to die from natural causes and subtracting this from 1. Lake trout data also included lamprey mortality rates, and the steelhead data included a spawning mortality rate. These additional mortality rates were combined with the natural and fishing mortality rates to be incorporated into their respective species model (Turschak et al., 2021; Lenart 2024).

Lake Whitefish

To calculate the survival probability for lake whitefish, the data for natural mortality and fishing mortality were used for all ages and calculated from the data available. For most units, the data provided was for fish ages 3-20+, however for units 3 and 4, the data was representative of ages 4-15 and 3-16 and all mortality rates were converted from instantaneous to discrete using equations that are representative of a type 2 fishery (Eq. T1.2.3 and Eq. T1.2.4). I used data from the most recent five years (2016-2020) to parameterize the model. The natural mortality rates for juvenile fish, lake whitefish ages 1 and 2, were assumed to be 30% because they experience similar levels of natural mortality to adults, usually within the range of 15-30% (Ebener, et al., 2021). For age 0 fish, the natural mortality rates are much higher as this is a highly sensitive stage in their lifecycle and they experience natural mortality at rates greater than 99% (Ebener et al., 2021).

To help capture the population level changes from PFAS exposure, the control Leslie matrix was adjusted to represent a stable population with no long-term growth or shrinkage (dominant eigenvalue = 1). This ensured that any changes in the population from the PFAS exposure simulations were from the contaminant itself and not because the control population was already growing or shrinking. To achieve a stable population with an eigenvalue equal to 1 ± 0.0001, the exact decimal of the age 0 natural mortality was manipulated while maintaining a value larger than 99.9%. Given the lack of data for juvenile fish from the lake whitefish datasets, the fishing mortality rates for ages 1 and 2 in all units, and age 3 for WFM03, were assumed to be equal to the rates found in the Technical Fisheries Committee Administrative Report from 2022 (Modeling Subcommittee, Technical Fisheries Committee, 2022). These fishing mortality rates were then converted from instantaneous to discrete rates (Eqs. T1.2.3 and T1.2.4).

The starting abundance for ages 3+, or 4+ for WFM03, came from average age specific abundance values from 2000-2020 in the SCA fisheries datasets (Newman et al., 2021). To calculate the starting abundance values for ages that did not have data available (ages 0-3 or 0-4 for management unit 3), we back projected abundance by dividing abundance at the next age class (N_{a+1}) by the survival rate for that age (S_a) (Eq. T1.2.5). This equation came from the Leslie matrix multiplication where each age class, N_a, is multiplied by the age specific survival probability, S_a, to find the population of the next age class at time t+1. For example, to calculate the age 2 abundance, the age 3 abundance from the lake whitefish dataset was divided by the survival probability of an age 2 fish surviving to reach age 3. This age 2 abundance was then divided by the age 1 survival probability to determine the age 1 abundance. Finally, the age 0 abundance was estimated by dividing the age 1 abundance by the age 0 survival probability.

Lake Trout

For the lake trout models, most of the data selection was the same as lake whitefish other than a few slight differences. The data for fishing, lamprey and natural mortality were all used in the calculation of the age specific survival probabilities and were all converted from instantaneous to discrete rates (Eqs. T1.1.3 and T1.1.4). Also, for each individual unit, the data available was for ages 1-15 between the years of 1985-2022. Although aging data stopped after 15, lake trout can live longer; these older fish were grouped into the 15+ category (Schram and Fabrizio, 1998). I assumed that age 0 fish had no fishing or lamprey induced mortality and the rate of natural mortality was also set to be >99% (Ebener et al., 2021). Similarly to the lake whitefish models, I manipulated the exact decimal value of the age 0 natural mortality so that the Leslie matrix had an eigenvalue of 1 ± 0.0001, to make it easier to discern which effects were from contaminants.

Steelhead Trout

The steelhead models represented ages 1 through 7+ between the years of 2000 through 2021, with the age specific natural mortality rates being selected from 2021. To include the spawning mortality data into this species model, it was multiplied by the proportion of mature fish in each age class, then it was added to the instantaneous fishing mortality for each age class and then converted to a discrete rate (Eq. T1.1.4). This rate was then subtracted from 1 along with the natural mortality rate to calculate the survival probability for each age class. Similarly to the previous two species, the age 0 natural mortality rate was set to be >99% with the specific decimal being selected to ensure the matrix had an eigenvalue of 1 ± 0.0001 and the abundance of age 0 fish was back calculated using the age 1 abundance and dividing by the age 0 survival probability (Eq. T1.2.5). The initial abundance values for steelhead trout came from average abundance values between 2000-2020 (Turschak et al., 2021).

2.5. DENSITY DEPENDENCE

To account for density dependent mortality affecting early life stages, I incorporated a Ricker stock-recruitment model into the Leslie matrix framework. The Ricker model estimates the expected number of recruits produced per year as a function of the number of spawners present in the population at time t using equation T1.2.6 where α is the maximum recruits-per-spawner and β represents density-dependent mortality. To quantify density dependence, I ran baseline simulations without stochasticity until the population reached stable age distribution and asymptotic abundance. The mean stable abundance of recruits was defined as the normalizing abundance (*norm)* for each species and management unit. At each yearly timestep, the Ricker equation predicted recruitment (R_t) and was compared to the normalizing abundance to create a recruitment adjustment multiplier (multiplier = $0.5 + 0.5 * R_t / norm$) following Diamond et al. (2013). This multiplier dynamically adjusted the survival probability of fish reaching the age of recruitment, which was age 3 for most models, but age 4 for WFM03 (due to absence of data for ages 0-3).

Estimation of Ricker model parameters used historical stock-recruitment datasets from Michigan Department of Natural Resources (Newman et al., 2021; Turschak et al., 2021; Lenart, 2024). First, annual estimates of spawner abundance and recruit abundance were compiled for each species and management unit over available time series. We then linearized the Ricker equation by dividing both sides by spawners and taking the natural logarithm: $\ln(R/S) = \ln(\alpha) - \beta S$ (T1.2.7). From the linearized equation, the beta value was equal to the slope and the natural log of alpha was equal to the y intercept before adjusting for bias correction. To make this bias correction adjustment to α, the residual standard error was squared, divided by two and added to the alpha value. This number was then exponentiated which resulted in the unbiased alpha value used in the model (Eq. T1.2.8).

Time series used for parameter estimation included: 1985–2018 for steelhead trout, all lake trout management units, and lake whitefish units WFM06 and WFM08, 1986–2017 for lake whitefish units WFM01, WFM02, WFM03, and WFM05, 1986–2005 for WFM04 and 1986–2009 for WFM05. Notably, WFM04 and WFM05 experienced pronounced declines in recruitment and spawner abundance beginning around 2000 and 2009, respectively, resulting in weak stock-recruit relationships that inflated time to stabilization beyond 75 years in preliminary model runs. To avoid unrealistic model behavior and to maintain comparability across units, we limited data used for parameter estimation in these two units to the periods prior to these declines, assuming pre-collapse dynamics better represented stable stock-recruit processes for these populations.

2.6. STOCHASTICITY

Stochasticity was incorporated into the model by adding random variation to the fecundity estimates used in the first row of the Leslie matrix. Specifically, each age-specific fecundity value was sampled annually from a normal distribution centered on its calculated mean (Eq. T1.2.2), with standard deviation determined from the coefficient of variation (CV). CVs were estimated separately for each species: for lake trout, variation in total abundance between 1985 and 2022 yielded unit-specific CVs ranging from 23.9% to 26.2%; for lake whitefish, fish production data from 2000–2020 produced a CV of 23.7% (Great Lakes Fisheries Commission, 2022); and for steelhead trout, abundance data from 2000–2021 gave a CV of 17.7%. These CVs were fine-tuned so that the model's simulated population abundances exhibited variability similar to observed stock assessment data. Incorporating stochasticity in this way added realistic, year-to-year uncertainty to the population projections.

2.7. PFAS EFFECTS

To incorporate PFAS effects into this population model, I constructed alternative Leslie matrices for fish assumed to be exposed to PFAS. To determine if a fish were exposed to PFAS or not, the parameter, percent_pfas, was set to a specific percentage of the population that was considered exposed. For each yearly iteration of the model, the entire population was multiplied by percent_pfas to ensure that each year, the same proportion of the population was exposed. This model used an assumption that the effects of PFAS were consistent across all age classes and that the exposure was constant throughout the duration of the model rather than bioaccumulating over time. The effects from PFAS contamination that were included in this matrix were: decreased egg survival, decreased weight at age, increased disease mortality and decreased eggs per kg (Appendix, Tables A1.12-A1.24).

To determine the PFAS effects, I used values estimated from literature focused on the impacts of PFAS on aquatic organisms, and I sought to find the common effects observed across all PFAS exposure levels and compound types. These effects were then grouped into categories of impacted egg survival, weight, disease mortality and other general effects from contamination. Based off the study duration, species, concentrations, compounds and % change from control to PFAS exposed, individual-PFAS effects were chosen. Egg survival was estimated from a study that followed a PFOA exposure of 2nM through water between hours 3-120 post fertilization and

8pM of PFOA through daily food aliquots between 1-6 months post fertilization. Results showed that embryo viability decreased by around 14% when compared to control fish (Jantzen et al., 2017). This study was also used to estimate reduced fecundity and reduced weight; control fish, produced 2184 eggs over the course of 9 breeding events and weighed around 0.4 grams whereas the PFOA exposed fish produced 1754 eggs and weighed around 0.29 grams (Jantzen et al., 2017), resulting in a 19.7% decrease in the eggs produced by the zebrafish exposed to PFAS while the weight of contaminated fish decreased by 27.5%.

There were several studies that showed specific immune related genes that were affected from PFAS exposure, which may increase susceptibility of becoming infected with various pathogens and potentially increasing the chance of disease mortality (Guillette et al., 2020; Hamibaugh et al., 2022; Zhang et al., 2020; Rodriguez et al., 2019). In a preliminary study looking at how PFOS exposure impacted lake trout infected with EEDV, there were increased mortalities among fish that were exposed to both PFOS and EEDV compared to the fish exposed to EEDV, but not to PFOS (Manliclic, Unpublished). To account for this in the model, it was assumed that there was a 20% increase in disease mortality compared to the baseline levels. I also assumed that the disease mortality was a component of the natural mortality, so to incorporate this parameter into the model for PFAS exposed fish, the disease mortality rate was subtracted from the natural mortality rate at each age. This left the natural mortality from anything other than disease. This increased disease mortality from PFAS exposure was then added back to that adjusted natural mortality value to create an increased natural mortality rate for fish exposed to PFAS. This effect was included in both matrix 2 and matrix 5 (Table 1.5). To test how these effects impacted the model outputs, five different matrices were used that included different combinations of these effects. Matrix 1 included all baseline levels other than the reduced eggs per kg, matrix 2 only included the increase disease mortality, matrix 3 only included the reduced weight at age, matrix 4 only included the reduced egg survival and matrix 5 included all four of these effects (Figure 1.4).

Table 1.5 Description of the Leslie matrix model simulations that were run for lake whitefish, lake trout and steelhead trout. Each simulation was run for 50 years and the model outputs showed total population abundance, abundance at each age and the egg abundance per year. These simulations were done for lake whitefish, lake trout and steelhead trout.

Simulations for Leslie Matrix Model

PFAS matrix used	Percent exposure		
1) Lower egg survival	0	50	100
2) Lower weight at age	0	50	100
3) Higher disease mortality	0	50	100
4) Lower eggs/kg	0	50	100
5) All effects	0	50	100

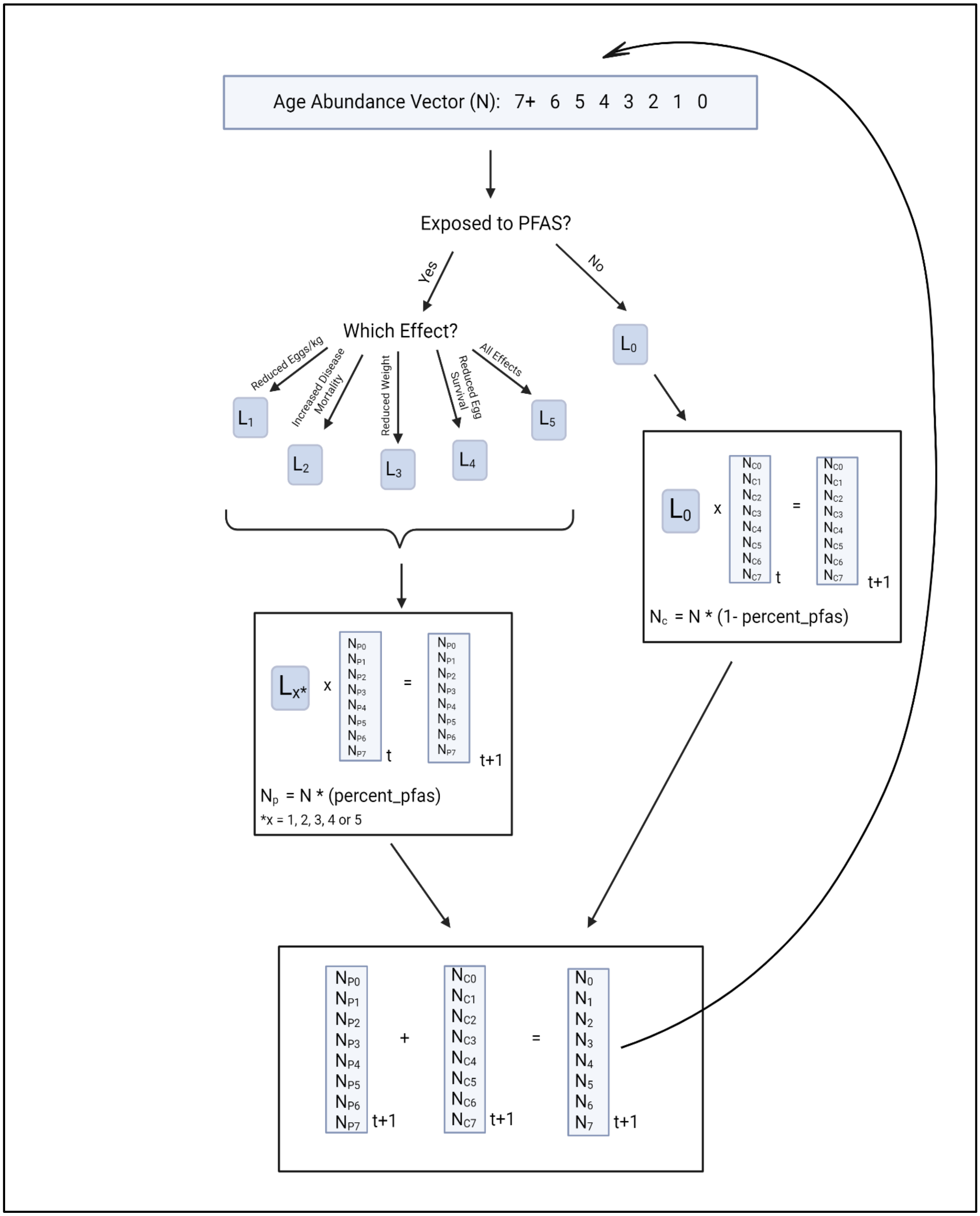

Figure 1.4 Population model structure throughout the yearly loop for ages 0-7+. The population is split into PFAS exposed and control populations and then multiplied by the corresponding Leslie matrix. The sum of the PFAS and control populations after the matrix multiplication is equal to the total population abundance for time t + 1. Created with BioRender.com.

2.8. SIMULATIONS

The same simulations were run for all three species using all 5 of the different PFAS matrices at different exposure levels (Table 1.5). For each specific matrix, the model was run with 0%, 50% and 100% of the population considered to be exposed to PFAS. For lake trout and lake whitefish, these simulations were done for each management unit individually. Each simulation scenario was run 3 times and the outputs from each run were averaged together prior to data analysis. The data used for analysis was taken from years 15-65 of the model after the total population abundance stabilized. The first 15 years were ignored to eliminate effects of initial conditions. Some lake whitefish units had weak stock-recruit relationships and their populations took longer to stabilize. The results for these units were still shown during the 15–65-year time period in order for the changes in population abundance to be comparable between species.

2.9. SENSITIVITY ANALYSIS

To identify which parameters had the largest effect on the output of total population abundance, a sensitivity analysis was conducted using all of the input parameters, these include, fishing mortality, disease mortality, natural mortality, maturity, weight at age, eggs/kg of spawning biomass, the ricker alpha parameter. For maturity, the sensitivity was only assessed if less than 60% of the fish reached maturity during that age class. For lake whitefish and lake trout, age 0-6 maturity was assessed and for steelhead, the ages of maturity that were assessed were ages 0-3. The local sensitivity of these parameters were determined using a coefficient of variation equal to 1%, 10% and 25%. The data selected for the simulations was used as the mean value for each parameter, and the coefficient of variation was used to solve for the resulting standard deviation at each level of variation for each parameter (Eq. T1.1.9). These standard deviations and mean parameter values were then used to sample from a normal distribution. At each level of variation, n=100 different samples were generated for each parameter. To account for the full range of variance for each parameter, the stratified sampling technique of Latin Hypercube Sampling was used. This technique divides up the potential parameter space into equal sections and selects one sample per section (Ivan et al., 2018).

To determine the local sensitivity of each parameter, the results from all 100 trials were plotted against the resulting population abundance average from years 15 through 65 of the model. The resulting R^2, coefficient of determination, was used to show how much variance in the model output was allocated to each parameter. If the R^2 value was greater than 0.2, the parameter was considered to be important (Ivan et al., 2018). This local sensitivity analysis was done using the control population matrix values.

3. RESULTS

3.1. MODEL VALIDATION

All species models exhibited variability in population abundance due to stochasticity in egg production. The coefficients of variation (CV) from lake trout abundance data were 26.1% for MM123, 24.7% from MM4, 23.9% from MM% and 24.9% from MM67. The resulting coefficients of variation from all three trials averaged together were 14.7% for MM123, 13% for MM4, 12.8% for MM5 and 13.2% for MM67. The CV from steelhead stock assessment data abundances was 17.7% and the resulting CV from the model output was 18.8%.

Lake whitefish abundances showed higher variability, with CVs of 40%-70% in wild populations (2005-2020) (Newman et al., 2021). Between 2005 and 2020, Lake Michigan wild whitefish populations declined by 64%-91% across all management units leading to this high variability in abundance over time (Newman et al., 2021; Ebener, 2021). The CV from lake whitefish production data in Lake Michigan was 23.7%; this value was used as the target CV for the model output data when running individual simulations of each management unit. The resulting CVs from the model abundance outputs of the baseline simulations were 19.0% for WFM01, 14.6% for WFM02, 18.8% from WFM03, 13.4% for WFM04, 14.5% for WFM05, 19.7% for WMF06, and 18.4% for WFM08.

3.2. LAKE WHITEFISH

The lake whitefish model simulated population abundance for ages 0-20+ and combined the results of each individual management unit to display the population dynamics occurring in Lake Michigan as a whole. The lowest population levels occurred when all effects were simulated, and 100% percent of the population was exposed to PFAS (Figure 1.5). The most significant individual effect was the reduced weight at age, followed by reduced egg per kg of fish. The increased disease mortality effect showed the lowest percent change in population and egg abundance; however, the population did continue to increase when this effect was modeled. The reduced egg survival also led to declines in average population abundance over this given period and altered the trajectory of the population from increasing growth to more stable levels fluctuating around 40 million for fish ages 1+ (Figure 1.5b).

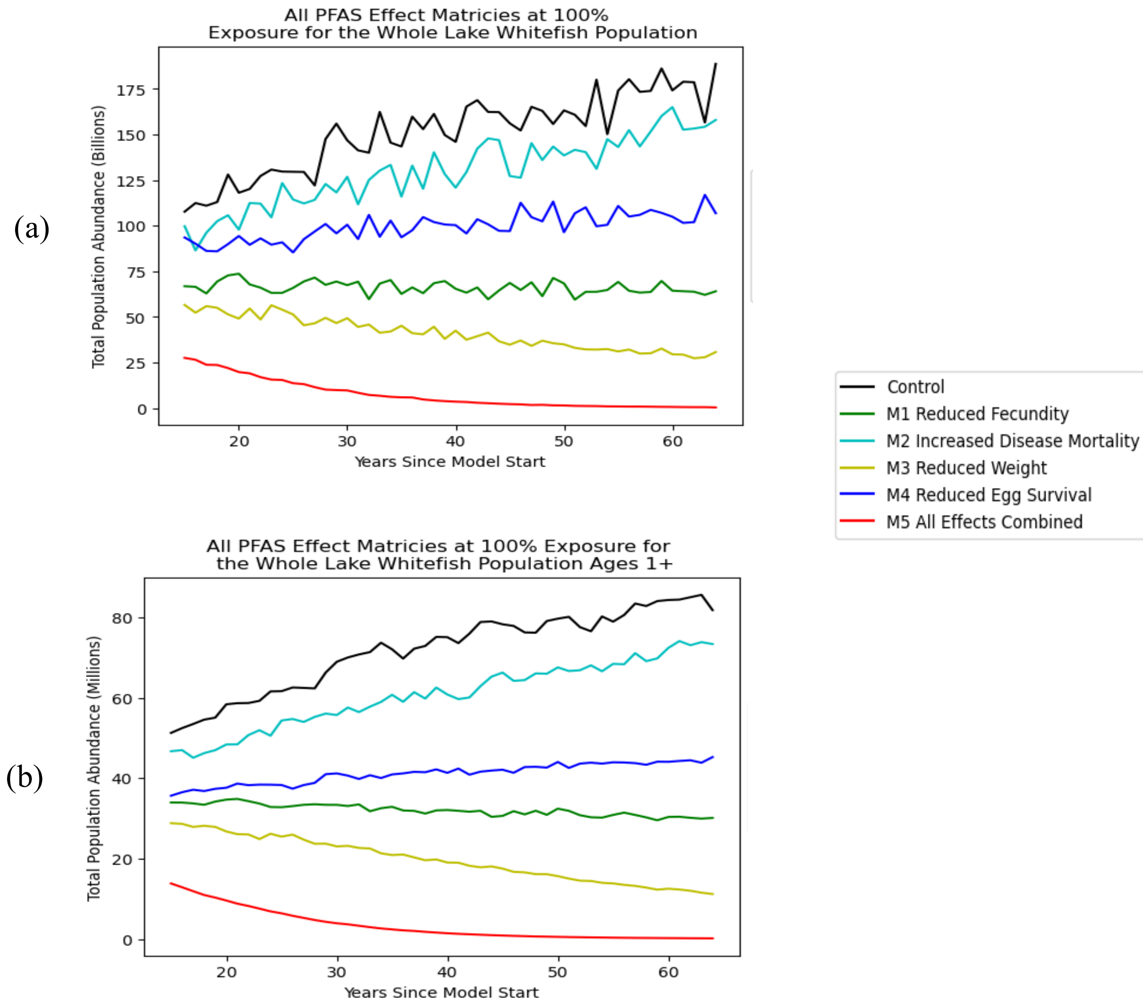

Figure 1.5 Average population abundances over the last 50 simulation years for 100% PFAS exposure. (a) Total abundance for ages 0-20+; (b) Total abundance excluding age-0 fish.

The lowest total abundance for fish ages 1+ was 3.36 ± 3.825 million under 100% exposure to all effects (Table 1.6). With 100% population exposure to reduced weight alone, average population abundance was 19.67 ± 5.39 million. This single effect caused a -72.6% decline in average population abundance of fish ages 1+ between years 15-65. The effect that led to the lowest percent change from baseline was the increased disease mortality. When 50% of the population was exposed to this effect, there was a -9.09% decline, and with 100% exposure there was a -15.58% decline from the average baseline abundance.

Table 1.6 Average population abundance (ages 0-20+ and 1-20+), egg abundance, and percent change from baseline for lake whitefish under various PFAS exposure scenarios.

PFAS Effect	Percentage of Population Exposed to PFAS	Total Population Abundance ± Standard Deviation (Billions)			Total Egg Abundance ± Standard Deviation (Billions)			Population Abundance Ages 1+ ± Standard Deviation (Millions)			Percent Change From Baseline	
											Egg Abundance	Population Abundance Ages 1+
Control	0%	151.161	±	21.137	151.090	±	21.129	71.840	±	9.804	0.000	0.000
Reduced Fecundity	50%	110.586	±	12.915	110.533	±	12.909	52.976	±	6.437	-26.842	-26.259
Reduced Fecundity	100%	66.082	±	3.361	66.050	±	3.360	32.080	±	1.408	-56.285	-55.345
Increased Disease Mortality	50%	140.195	±	21.606	140.130	±	21.596	65.305	±	10.086	-7.254	-9.097
Increased Disease Mortality	100%	129.746	±	18.580	129.685	±	18.572	60.646	±	8.228	-14.167	-15.583
Reduced Weight	50%	91.679	±	8.497	91.635	±	8.494	43.589	±	3.560	-39.350	-39.325
Reduced Weight	100%	40.932	±	8.666	40.912	±	8.661	19.668	±	5.387	-72.922	-72.623
Reduced Egg Survival	50%	129.462	±	18.122	129.405	±	18.115	57.314	±	8.022	-14.352	-20.221
Reduced Egg Survival	100%	99.614	±	7.406	99.573	±	7.404	41.152	±	2.508	-34.097	-42.718
All Effects	50%	41.630	±	9.641	41.612	±	9.636	18.067	±	5.541	-72.459	-74.852
All Effects	100%	7.356	±	7.840	7.353	±	7.836	3.360	±	3.825	-95.134	-95.323

The percent change analysis showed decreased egg and population abundance from all exposure levels to all effects, both individually modeled, and all effects combined (Figures 1.6, 1.7). The largest decline in average egg abundance from a single effect occurred in the reduced weight simulation with a 100% population exposure (-72.9%). This effect also led to the largest decline in egg abundance (-39.4%) when only 50% of the population was exposed to PFAS effect (Table 1.6, Figure 1.6). For both egg and population abundance of fish ages 1+, there were similar percent changes values for all effects besides the reduced egg survival simulations. This reduction of egg survival resulted in larger declines of percent change for population abundance compared to egg abundance for both 50% and 100% population exposures (Table 1.6, Figure 1.6, 1.7).

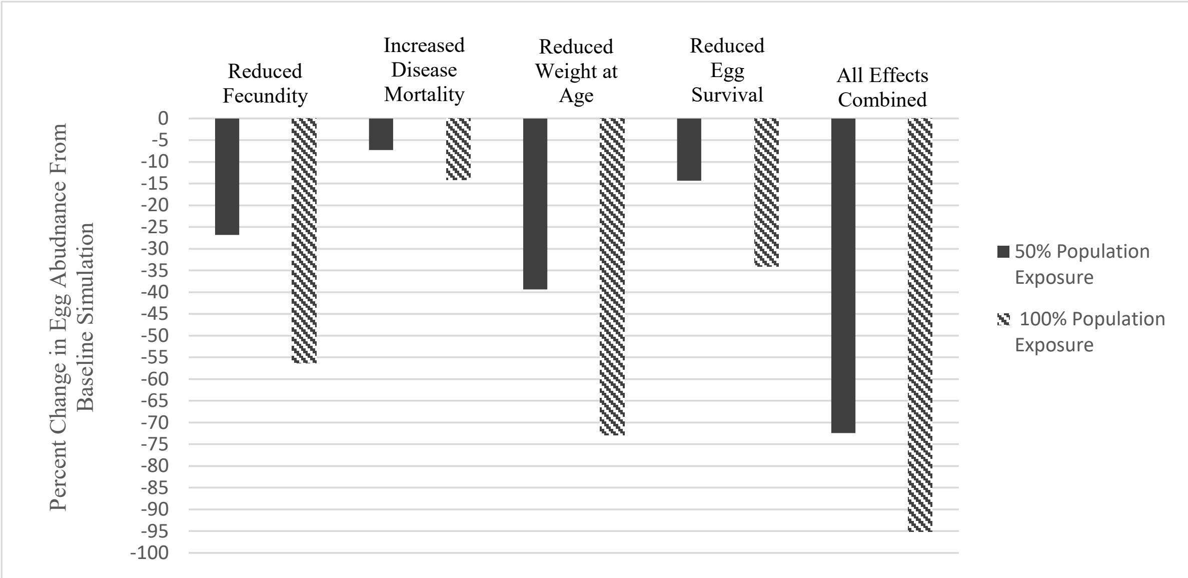

Figure 1.6 Percent change in average egg abundance under varying PFAS exposure levels.

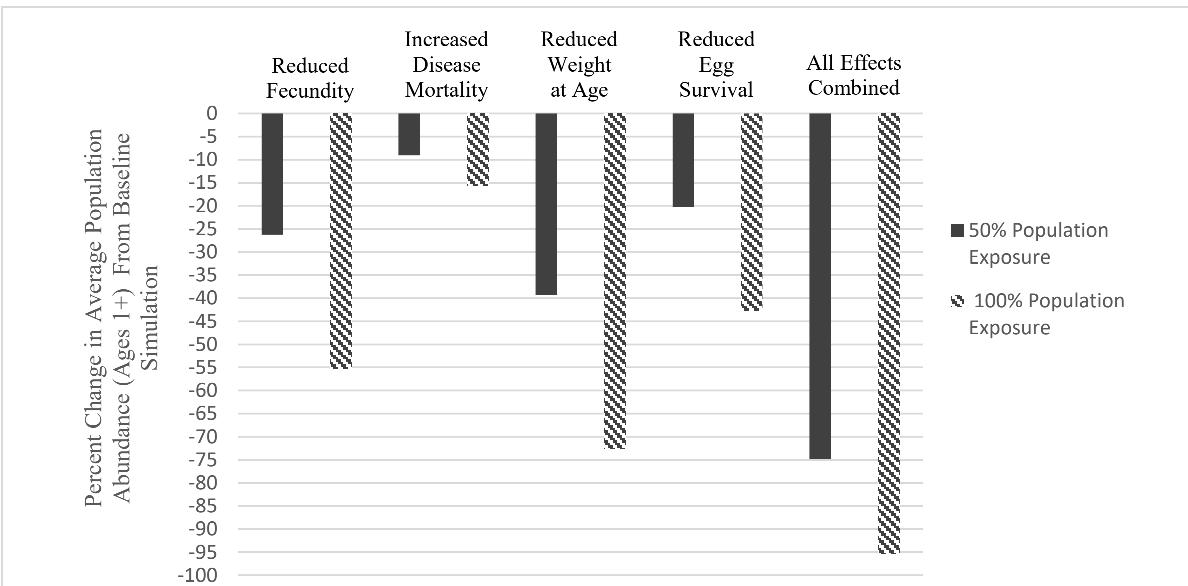

Figure 1.7 Percent change in average population abundance (excluding age 0) under varying PFAS exposure levels.

The sensitivity analysis identified age-0 natural mortality as the most influential parameter across all management units, with R^2 values exceeding 0.2. WFM-02 was the only unit that showed an R^2 value of 0.1042 or 10.14% for age 3 natural mortality (Table 1.7).

Table 1.7 Variance explained (R^2) between parameters and average total population abundance from model years 15-65 for all lake whitefish management units. Bolded values showed the highest R^2 parameters, whereas those underlined show R^2 values between 10 and 20%. Parameters were only included in this table if the R^2 was larger than 0.05 or 5% for at least one CV.

Lake Whitefish Sensitivity Analysis

Management Unit	Parameters	1% CV	10% CV	25% CV
		Average Total Population Abundance from Years 20-50		
WFM01	Age 0 Natural Mortality	0.1517	**0.2846**	0.0820
	Age 13 Natural Mortality	0.0277	0.0719	0.0089
	Age 20+ Natural Mortality	0.0920	0.0030	0.0068
	Age 8 Fishing Mortality	0.0209	0.0635	0.0300
	Age 11 Fishing Mortality	0.0054	0.0379	0.0556
WFM02	Age 0 Natural Mortality	**0.2299**	**0.2703**	**0.2234**
	Age 3 Natural Mortality	0.0000	0.1042	0.0095
	Age 12 Natural Mortality	0.0083	0.0222	0.0587
	Age 4 Fishing Mortality	0.0532	0.0223	0.0040
	Age 7 Fishing Mortality	0.0067	0.0049	0.0534
WFM03	Age 0 Natural Mortality	0.1974	**0.2358**	0.0870
	Age 8 Weight	0.0946	0.0244	0.0062
	Age 12 Fishing Mortality	0.0600	0.0016	0.0130
WFM04	Age 0 Natural Mortality	**0.2230**	0.0772	0.1493
	Age 2 Natural Mortality	0.0000	0.0401	0.0513
	Age 4 Weight	0.0029	0.0686	0.0022
	Age 10 Weight	0.0395	0.0052	0.0584
	Age 11 Weight	0.0622	0.0010	0.0410
	Age 9 Fishing Mortality	0.0555	0.0016	0.0110
WFM05	Age 0 Natural Mortality	**0.2029**	0.1734	**0.2227**
	Age 2 Natural Mortality	0.0870	0.0156	0.0004
	Age 5 Maturity	0.0199	0.0587	0.0058
	Age 19 Weight	0.0110	0.0000	0.0854
	Age 1 Fishing Mortality	0.0212	0.0082	0.0615
	Age 12 Fishing Mortality	0.0603	0.0000	0.0000
WFM06	Age 0 Natural Mortality	**0.2028**	0.1079	0.1080
	Age 1 Natural Mortality	0.0113	0.0136	0.0551
	Age 7 Natural Mortality	0.0520	0.0003	0.0017
	Age 8 Natural Mortality	0.0187	0.0551	0.0011
	Age 20+ Natural Mortality	0.0564	0.0024	0.0015
	Disease Mortality	0.0548	0.0008	0.0039
	Age 10 Weight	0.0064	0.0748	0.0000
	Eggs per Kg	0.0038	0.0892	0.0081
WFM08	Age 0 Natural Mortality	0.1843	**0.2459**	0.1049
	Age 3 Natural Mortality	0.0723	0.0123	0.0041
	Age 9 Natural Mortality	0.0005	0.0136	0.0819
	Age 6 Fishing Mortality	0.0254	0.0570	0.0443
	Age 7 Fishing Mortality	0.0780	0.0010	0.0062

3.3. LAKE TROUT

The lake trout model simulated abundance for ages 0-15+ and combined the results of each individual management unit to display the population dynamics occurring in Lake Michigan as a whole. The lowest population levels occurred under combined PFAS effects (Figure 1.8). Reduced weight at age had the greatest individual impact, followed by reduced eggs per kg. All effects at the 100% population exposure level caused the trend of the overall population to decline compared to the trajectory of the stable, baseline population (Figure 1.8).

(a)

(b)

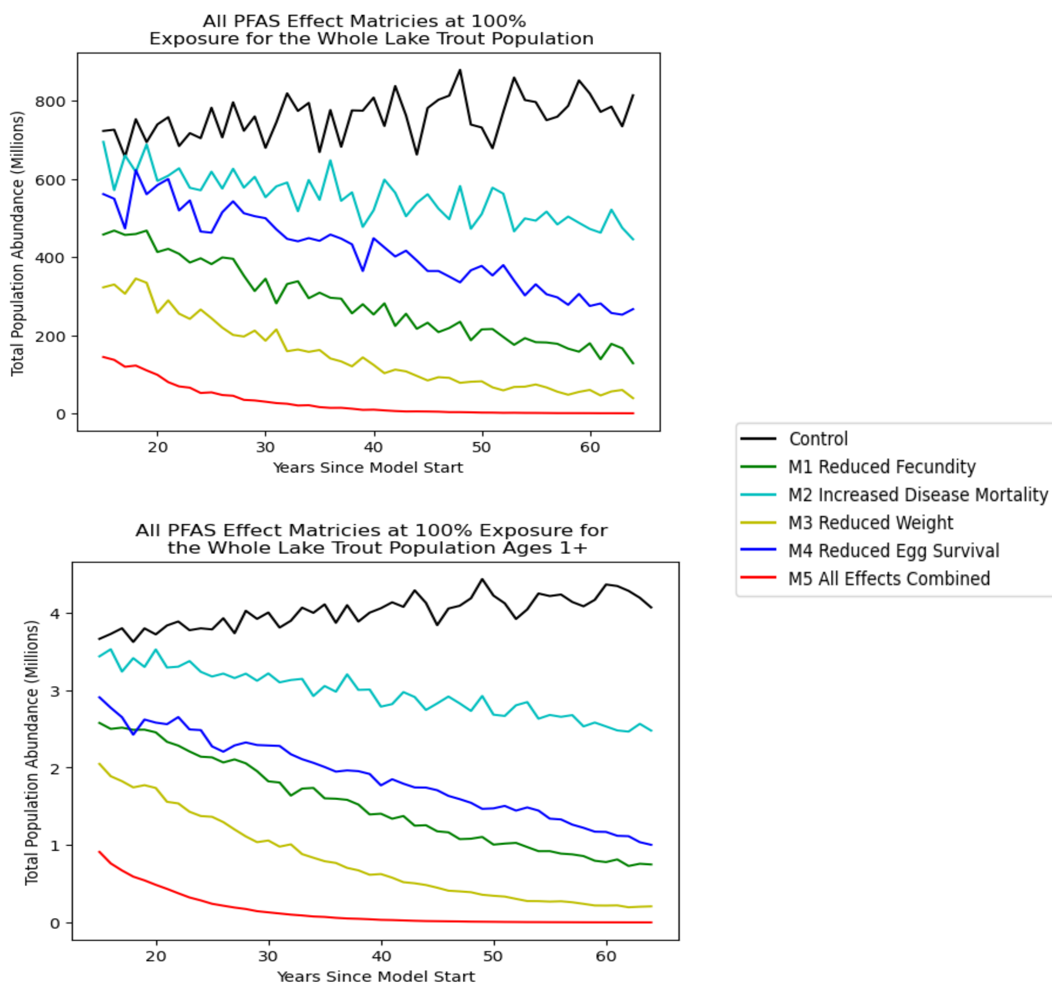

Figure 1.8 Average population abundances over the last 50 simulation years for 100% PFAS exposure. (a) Total abundance for ages 0-15+; (b) Total abundance excluding age-0 fish.

Baseline egg abundance was 755.204 ± 52.409 million and baseline population abundance was 4.013 ± 0.195 million for ages 1+ (Table 1.8). The individual effect that caused the largest decline to egg and population abundance was the reduced weight at age. At a 100% population exposure, this effect lowered the average egg abundance to 148.638 ± 89.446 (-606.566 million from baseline) and average population abundance of ages 1+ to 0.796 ± 0.548 million (-3.217 million from baseline). All effects at 50% and 100% exposure levels resulted in over -10% declines to both egg and population abundance from baseline conditions (Table 1.8). The largest percent declines for egg and population abundance came from the simulation of all effects at 100% population exposure. Egg abundance showed a -96.147% decline and population abundance of ages 1+ showed a -96.322% decline. (Table 1.8, Figures 1.8, 1.9).

Table 1.8 Average population abundance (ages 0-20+ and 1-20+), egg abundance, and percent change from baseline for lake trout under various PFAS exposure scenarios.

PFAS Effect	Percentage of Population Exposed to PFAS	Total Population Abundance ± Standard Deviation (Millions)			Total Egg Abundance ± Standard Deviation (Millions)			Population Abundance Ages 1+ ± Standard Deviation (Millions)			Percent Change From Baseline	
											Egg Abundance	Population Abundance Ages 1+
Control	0%	759.218	±	52.455	755.204	±	52.409	4.013	±	0.195	0.000	0.000
Reduced Fecundity	50%	475.374	±	70.535	472.830	±	70.161	2.544	±	0.402	-37.390	-36.613
Reduced Fecundity	100%	283.267	±	99.941	281.746	±	99.367	1.522	±	0.585	-62.693	-62.088
Increased Disease Mortality	50%	665.667	±	33.722	662.110	±	33.727	3.557	±	0.091	-12.327	-11.361
Increased Disease Mortality	100%	553.637	±	59.986	550.677	±	59.778	2.961	±	0.294	-27.082	-26.230
Reduced Weight	50%	366.884	±	90.962	364.922	±	90.439	1.962	±	0.539	-51.679	-51.107
Reduced Weight	100%	149.434	±	89.987	148.638	±	89.446	0.796	±	0.548	-80.318	-80.166
Reduced Egg Survival	50%	567.792	±	57.968	564.922	±	57.758	2.870	±	0.258	-25.196	-28.488
Reduced Egg Survival	100%	418.704	±	98.530	416.820	±	98.044	1.884	±	0.516	-44.807	-53.064
All Effects	50%	152.802	±	93.059	152.065	±	92.533	0.737	±	0.529	-79.864	-81.639
All Effects	100%	29.245	±	39.904	29.097	±	39.685	0.148	±	0.221	-96.147	-96.322

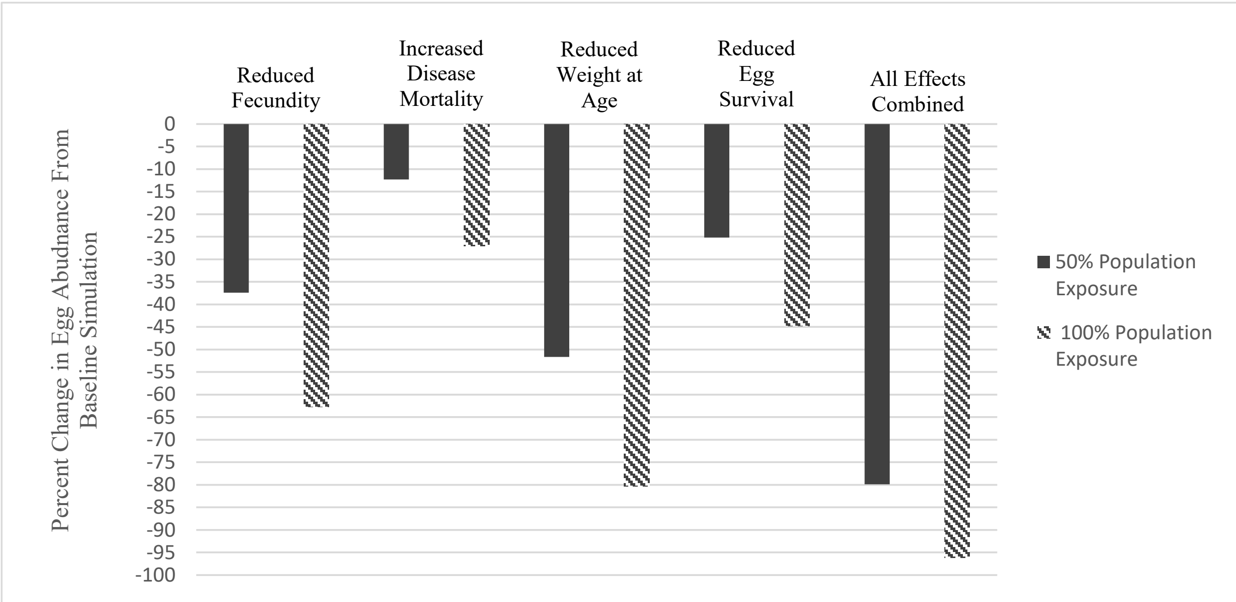

Figure 1.9 Percent change in egg abundance under varying PFAS exposure levels.

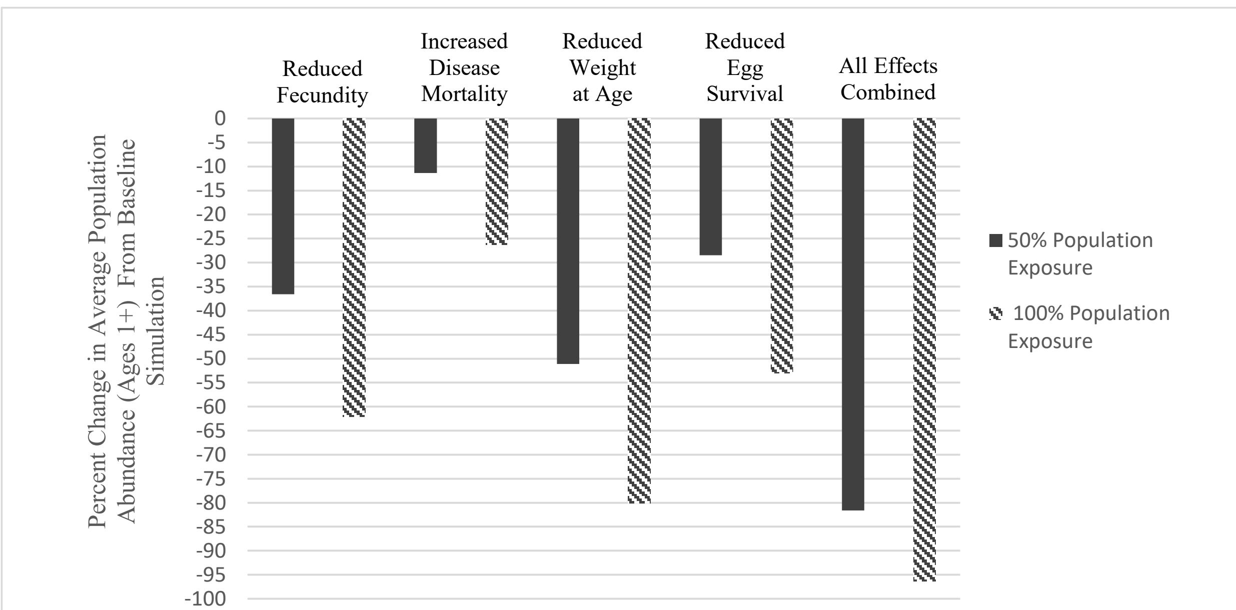

Figure 1.10 Percent change in total population abundance (excluding age 0) under varying PFAS exposure levels.

The sensitivity analysis showed that age 0 natural mortality was the most sensitive parameter across all management units with an R^2 values exceeding 0.2 (Table 1.9). MM-5 was the only unit to show an R^2 value of 0.1017 or 10.17% for age 4 fishing mortality.

Table 1.9 Variance explained (R^2) between parameters and average total population abundance from model years 15-65 for all lake trout management units. Bolded values showed the highest R^2 parameters, whereas those underlined show R^2 values between 10 and 20%. Parameters were only included in this table if the R^2 was larger than 0.05 or 5% for at least one CV.

Lake Trout Sensitivity Analysis

Management Unit	Parameters	1% CV	10% CV	25% CV
		Average Total Population Abundance from Years 20-50		
MM123	Age 0 Natural Mortality	<u>0.1977</u>	0.0918	0.0221
	Age 2 Natural Mortality	0.0027	0.0735	0.0439
	Disease Mortality	0.0004	0.0129	0.0698
	Age 5 Maturity	0.0001	0.0770	0.0107
	Ricker Alpha	0.0017	0.0741	0.0002
	Age 12 Fishing Mortality	0.0064	0.0030	0.0541
MM4	Age 0 Natural Mortality	**0.2058**	<u>0.1577</u>	<u>0.1032</u>
	Age 3 Natural Mortality	0.0507	0.0180	0.0017
	Age 4 Maturity	0.0845	0.0377	0.0108
	Age 5 Weight	0.0259	0.0109	0.0718
	Age 11 Fishing Mortality	0.0114	0.0506	0.0016
	Age 14 Fishing Mortality	0.0039	0.0000	0.0600
MM5	Age 0 Natural Mortality	**0.2565**	0.0960	**0.2308**
	Age 3 Natural Mortality	0.0063	0.0791	0.0006
	Age 7 Natural Mortality	0.0017	0.0578	0.0027
	Age 10 Natural Mortality	0.0156	0.0589	0.0130
	Age 13 Weight	0.0571	0.0022	0.0004
	Eggs per Kg	0.0159	0.0028	0.0625
	Age 4 Fishing Mortality	0.0033	<u>0.1017</u>	0.0070
	Age 9 Fishing Mortality	0.0323	0.0091	0.0564
	Age 11 Fishing Mortality	0.0592	0.0008	0.0237
MM67	Age 0 Natural Mortality	**0.2150**	<u>0.1049</u>	0.0793
	Age 3 Natural Mortality	0.039667	0.023464	0.066149

3.4. STEELHEAD TROUT

The steelhead trout model simulated abundance estimates for ages 0-7+ (Figure 1.11). Combined PFAS effects led to the lowest population levels and caused significant declines within the first 15 years shown in Figure 1.11. Reduced weight at age and reduced fecundity had the greatest individual impacts, although all effects individually led to lower populations throughout the 65 year simulation. The increased disease mortality altered the population abundance the least compared to the other individual effects. When ages 0+ were modeled (Figure 1.11a), the disease mortality abundance levels were similar to those of the baseline simulation between years 40-65; however, when the age 0 fish were not included, and only ages 1+ were plotted, the difference in abundances were more clear to see (Figure 1.11b).

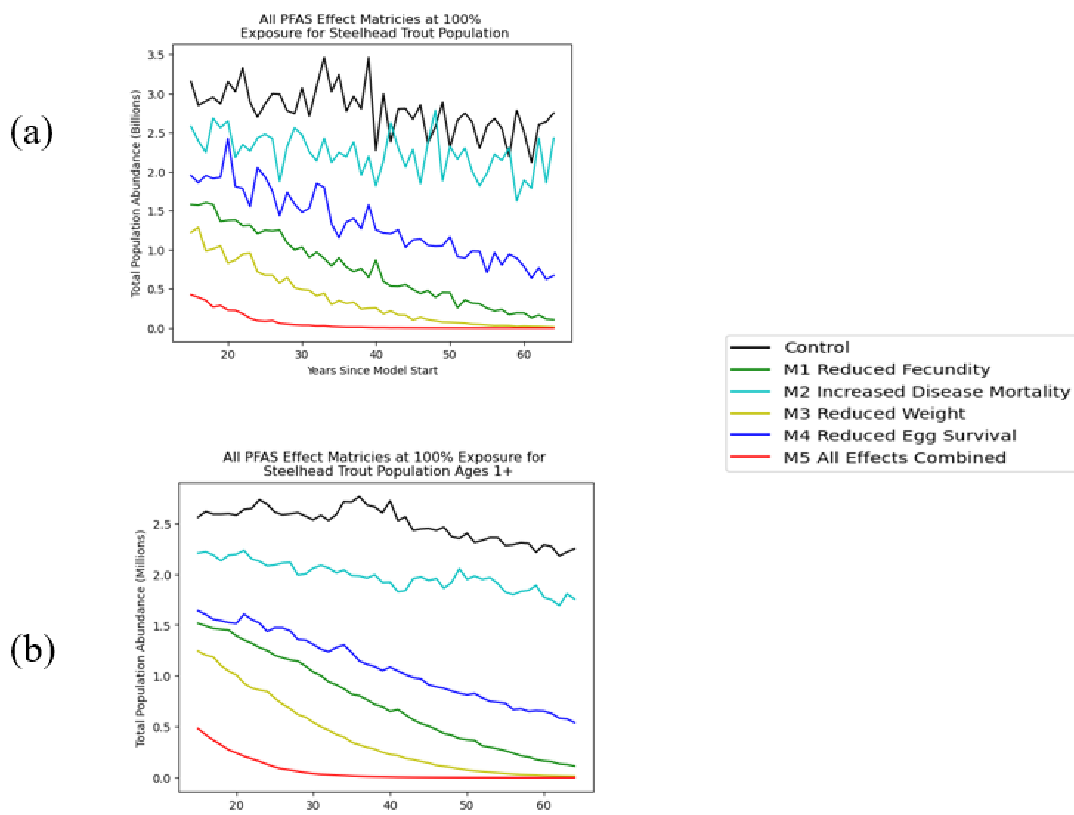

Figure 1.11 Average population abundances over the last 50 simulation years for 100% PFAS exposure. (a) Total abundance for ages 0-7+; (b) Total abundance excluding age-0 fish.

The largest single-effect decline in egg abundance (-86.69%) occurred under 100% reduced weight exposure (Table 1.10). Combined effects at 100% exposure resulted in a -97.76% decline in egg abundance and a -97.278% decrease in population abundance of fish ages 1+ (Table 1.10, Figures 1.12, 1.13).

Table 1.10 Average population abundance (ages 0-20+ and 1-20+), egg abundance, and percent change from baseline for steelhead trout under various PFAS exposure scenarios.

PFAS Effect	Percentage of Population Exposed to PFAS	Total Population Abundance ± Standard Deviation (Billions)			Total Egg Abundance ± Standard Deviation (Billions)			Population Abundance Ages 1+ ± Standard Deviation (Millions)			Percent Change From Baseline	
											Egg Abundance	Population Abundance Ages 1+
Control	0%	2.790	±	0.301	2.787	±	0.301	2.493	±	0.161	0.000	0.000
Reduced Fecundity	50%	1.496	±	0.298	1.494	±	0.298	1.413	±	0.273	-46.392	-43.302
Reduced Fecundity	100%	0.746	±	0.468	0.746	±	0.468	0.739	±	0.454	-73.247	-70.337
Increased Disease Mortality	50%	2.433	±	0.201	2.430	±	0.201	2.183	±	0.098	-12.809	-12.446
Increased Disease Mortality	100%	2.235	±	0.265	2.233	±	0.265	1.981	±	0.137	-19.874	-20.532
Reduced Weight	50%	1.333	±	0.350	1.332	±	0.349	1.277	±	0.331	-52.230	-48.784
Reduced Weight	100%	0.371	±	0.369	0.371	±	0.369	0.391	±	0.386	-86.689	-84.299
Reduced Egg Survival	50%	1.818	±	0.282	1.816	±	0.282	1.581	±	0.230	-34.849	-36.581
Reduced Egg Survival	100%	1.331	±	0.443	1.330	±	0.443	1.087	±	0.342	-52.297	-56.395
All Effects	50%	0.384	±	0.385	0.384	±	0.385	0.371	±	0.372	-86.228	-85.110
All Effects	100%	0.062	±	0.111	0.062	±	0.111	0.068	±	0.120	-97.763	-97.278

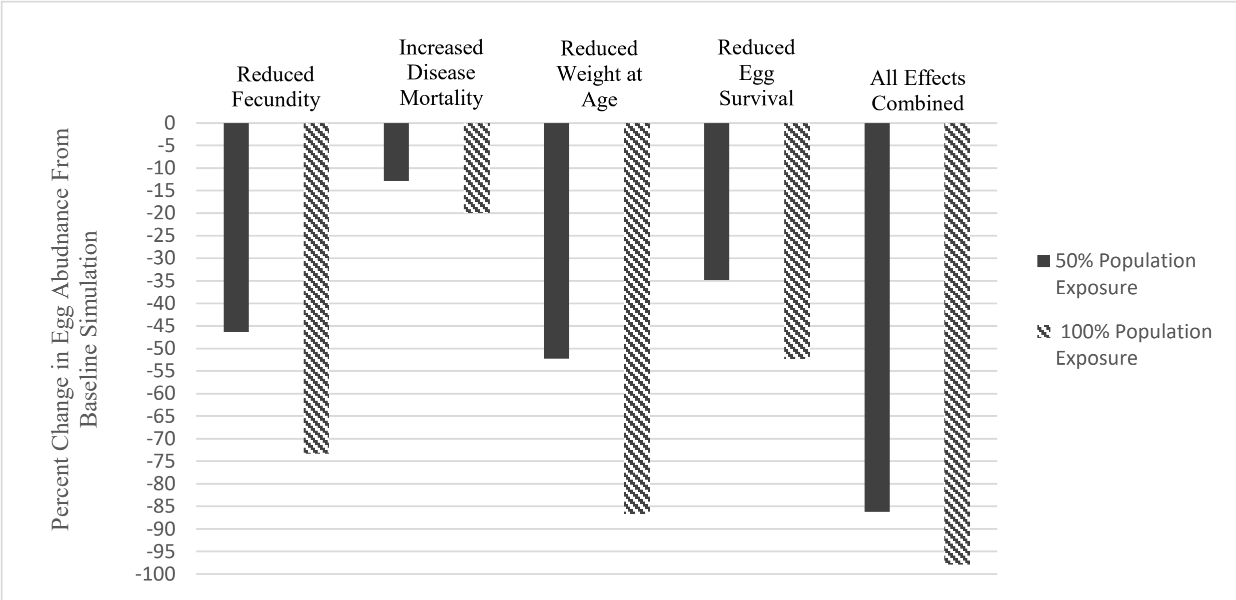

Figure 1.12 Percent change in average egg abundance under varying PFAS exposure levels.

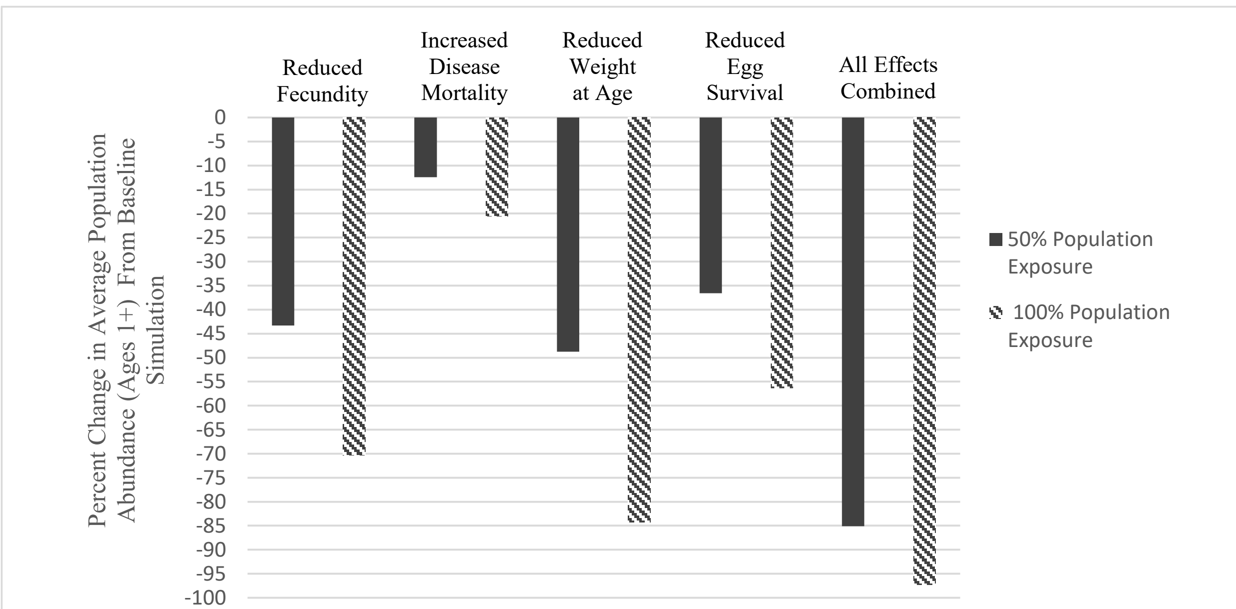

Figure 1.13 Percent change in average population abundance (excluding age 0) under varying PFAS exposure levels.

The sensitivty analysis found that age 0 natural mortality was the only parameter with an R^2 value larger than 0.1 or 10%. No parameters has R^2 values larger than 0.2 or 20% (Table 1.11).

Table 1.11 Variance explained (R^2) between parameters and average total population abundance from model years 15-65 for steelhead trout. Bolded values showed the highest R^2 parameters, whereas those underlined show R^2 values between 10 and 20%. All parameters tested in the sensitivity analysis were included in this table.

Steelhead Trout			
Parameters	1% CV	10% CV	25% CV
	Average Total Population Abundance from Years 15-65		
Age 1 Fishing Mortality	0.0070	0.0619	0.0109
Age 2 Fishing Mortaltiy	0.0081	0.0001	0.0050
Age 3 Fishing Mortality	0.0679	0.0108	0.0011
Age 4 Fishing Mortality	0.0007	0.0178	0.0035
Age 5 Fishing Mortality	0.0034	0.0036	0.0069
Age 6 Fishing Mortality	0.0004	0.0182	0.0000
Age 7 Fishing Mortality	0.0208	0.0000	0.0025
Age 0 Natural Mortality	0.1619	0.1367	0.1113
Age 1 Natural Mortality	0.0197	0.0139	0.0001
Age 2 Natural Mortality	0.0349	0.0002	0.0173
Age 3 Natural Mortality	0.0009	0.0127	0.0058
Age 4 Natural Mortality	0.0145	0.0009	0.0223
Age 5 Natural Mortality	0.0153	0.0165	0.0037
Age 6 Natural Mortality	0.0026	0.0011	0.0593
Age 7 Natural Mortality	0.0005	0.0001	0.0034
Disease Mortality	0.0037	0.0059	0.0201
Age 1 Maturity	0.0072	0.0061	0.0533
Age 2 Maturity	0.0671	0.0319	0.0016
Age 1 Weight	0.0049	0.0087	0.0364
Age 2 Weight	0.0004	0.0033	0.0133
Age 3 Weight	0.0170	0.0196	0.0008
Age 4 Weight	0.0939	0.0001	0.0103
Age 5 Weight	0.0002	0.0052	0.0003
Age 6 Weight	0.0000	0.0003	0.0001
Age 7 Weight	0.0049	0.0219	0.0045
Eggs per Kg	0.0005	0.0072	0.0021
Ricker Alpha	0.0009	0.0244	0.0324

3.5. COMPARISON BETWEEN SPECIES

Among all species and management units, reduced weight at age and reduced fecundity caused the largest declines in population and egg abundance (Figures 1.14, 1.15). Combined effects at 100% exposure led to the largest declines across species. For reduced weight, reduced eggs per kg and reduced egg survival, the largest declines in percent change were found in steelhead trout for both egg and population abundance at 100% population exposure. The 100% population exposure to increased disease mortality led to the largest declines in population abundance in lake trout (-26.23%), followed by steelhead trout (-20.53%) and lake whitefish (-15.58%). The 100% exposure to reduced fecundity led to the largest percent declines in steelhead trout (-70.343%), compared to lake trout (-62.09%), and lake whitefish (-55.35%).

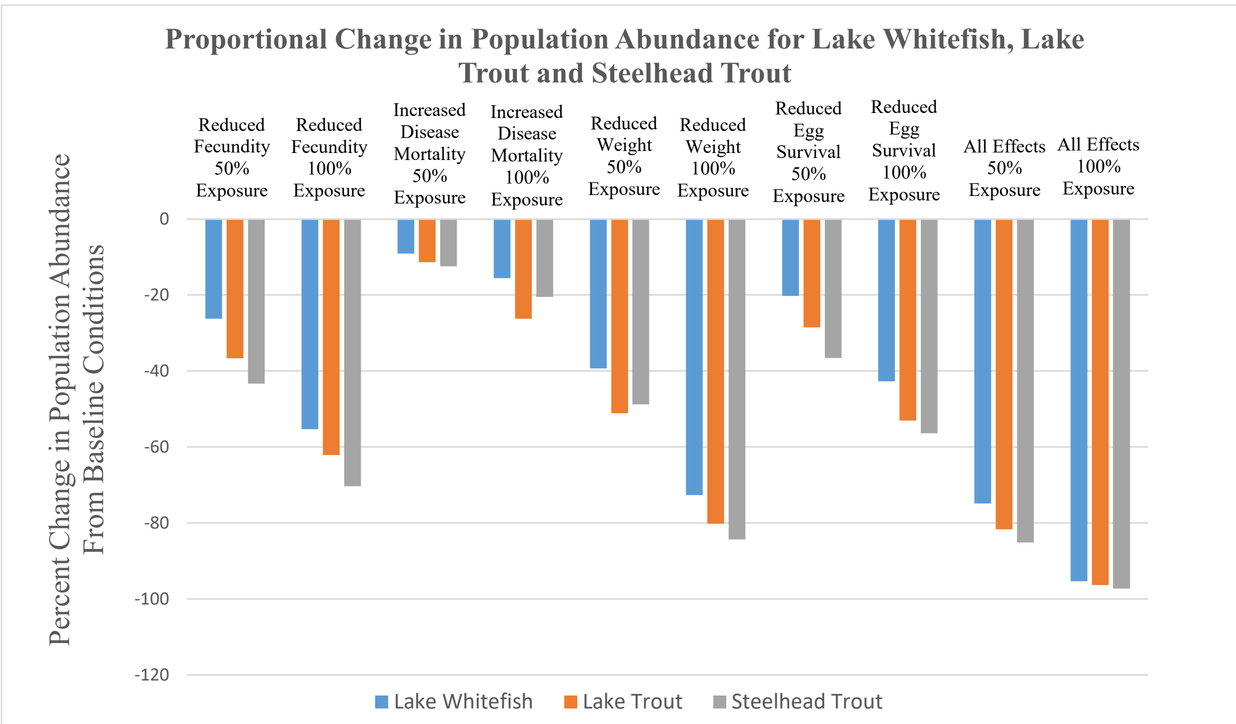

Figure 1.14 Percent change in total population abundance (ages 1+) for all species under varying PFAS exposure levels.

Similarly to population abundance, egg abundance showed the largest decreases in lake trout for 100% exposure to increased disease mortality. Steelhead also showed the largest declines in 100% exposures to reduced fecundity, reduced weight and reduced egg survival. For all effects, lake whitefish showed the lowest percent change compared to steelhead trout and lake trout.

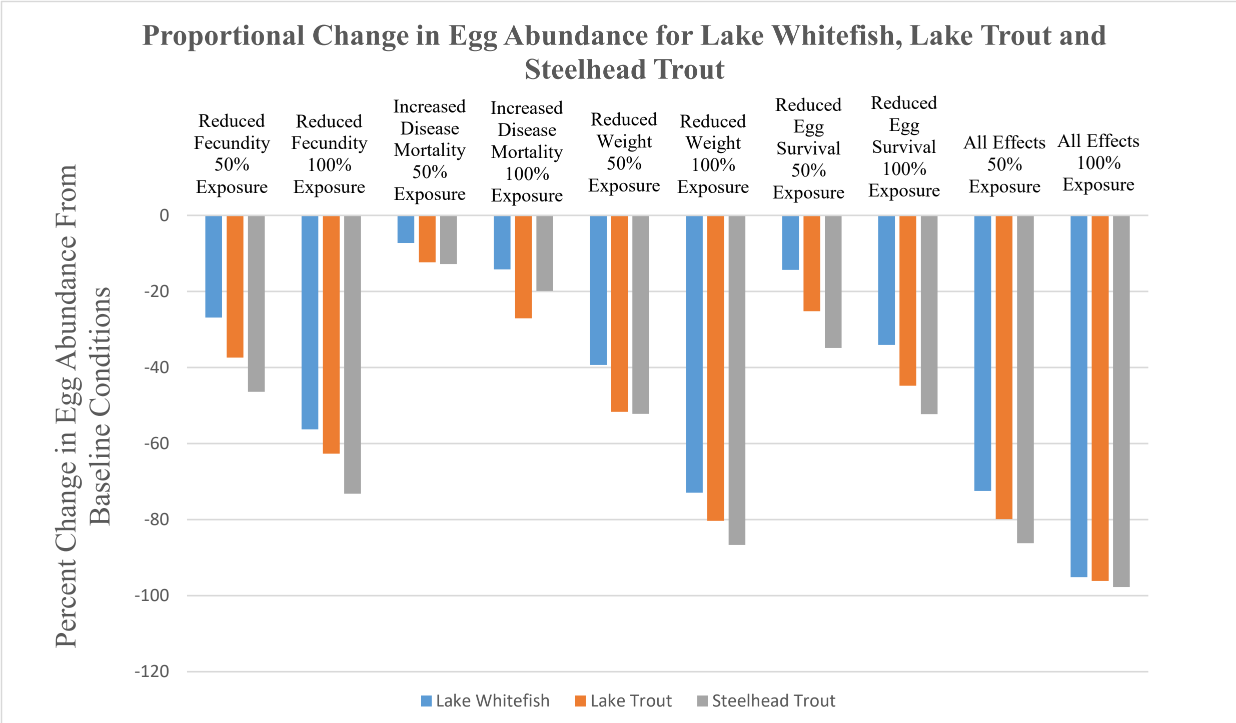

Figure 1.15 Percent change in egg abundance for all species under varying PFAS exposure levels.

All three species showed similar results for the sensitivity analysis with age 0 natural mortality being the most sensitive parameter in terms of impacting the average total population abundance output.

4. DISCUSSION

This chapter bridges the gap between toxicological research on PFAS exposure and population-level effects by incorporating observed sublethal PFAS impacts into discrete, age-structured models for three key freshwater fish species: lake whitefish, lake trout, and steelhead trout. The simulation results showed that across all three species, the reduction in weight at age had the greatest impact on population abundance, consistent with the assumption of shared PFAS effects among species. This reliance on zebrafish-derived PFAS effects highlights the need for species-specific toxicity studies, as there is limited research directly examining PFAS impacts on Great Lakes fish.

Reduced fecundity, implemented as a 19.7% decrease in eggs per kilogram of spawning biomass (Jantzen et al., 2017), also significantly reduced both egg production and population abundance. This is consistent with studies showing that fish reproductive output increases with size (Barneche et al., 2018); thus, impaired growth reduces fecundity and recruitment. Similar growth and reproductive inhibition have been documented in zebrafish exposed to other PFAS compounds, such as F-53B (Shi et al., 2018).

While reduced weight and fecundity consistently had the largest impacts across species, species-specific sensitivity emerged in model outputs. Lake whitefish exhibited the smallest relative declines, likely because of their larger baseline population size (mean 71.84 ± 9.8 million age-1+ fish) and higher egg production rates, which buffer population-level impacts. In contrast, steelhead trout experienced the largest declines under most individual PFAS effects, potentially due to their smaller population size, exclusion of stocking in the model, lower eggs-per-kilogram, and fewer spawning age classes. Lake trout were most impacted by increased disease mortality when 100% of the population was exposed.

As expected, simulations where all PFAS effects acted simultaneously and 100% of the population was exposed produced the most dramatic declines—over 95% reduction in population and egg abundance across all three species. This finding emphasizes the importance of modeling combined sublethal effects, as single-effect simulations risk severely underestimating population impacts.

These results underscore the need for holistic modeling efforts incorporating multiple interacting stressors, since PFAS can simultaneously disrupt reproduction, growth, and survival—three critical determinants of population persistence. Moreover, as new research clarifies PFAS effects on reproduction, immunity, and development in aquatic species, models must be updated with refined, species-specific parameters to avoid underestimating population risks.

Importantly, in real ecosystems, PFAS does not act in isolation. Additional stressors—such as microplastics, climate change, and other pollutants—may compound PFAS effects. For example, Huang et al. (2013) demonstrated in rainbow trout that chemical contamination by mercury increased mortality and reduced reproduction, causing nearly linear declines in population biomass with increasing contaminant concentration. This precedent highlights the need for future PFAS modeling efforts to incorporate variable exposure concentrations, compound mixtures, and interactive stressors to reflect real-world complexity.

This model represents, to our knowledge, the first attempt to directly link sublethal PFAS toxicological effects to fish population dynamics. Current literature relies heavily on zebrafish data (e.g., Jantzen et al., 2016, 2017; Haimbaugh et al., 2022), underscoring the urgent need for studies measuring PFAS impacts on lake whitefish, lake trout, and steelhead trout specifically.

4.1. LIMITATIONS

Key limitations of this work include the use of toxicity estimates from zebrafish as surrogates for Great Lakes species, assuming PFAS effects were static throughout the model simulation and the exclusion of potential density-independent stressors or compensatory dynamics (e.g., reduced competition at low abundance). Another limitation was that the PFAS effects modeled in this chapter resulted from exposure to either PFOA or PFOS, but in real world environments, fish are likely exposed to these compounds in mixtures that can increase toxicity compared to single compound exposures (Liu et al., 2022, Environmental Protection Agency, 2022, as cited in Miranda et al., 2023). Additionally, the model did not include potential management interventions, such as adjusted harvest regulations, invasive species control, gear restrictions, or increased stocking, which could influence real population trajectories in response to PFAS-related declines.

4.2. IMPLICATIONS FOR MANAGMENT

Despite these limitations, the modeling framework developed here provides a valuable tool for fisheries managers and policymakers to anticipate the potential long-term impacts of PFAS contamination on key fish populations. As more research becomes available, incorporating species-specific PFAS effects, mixture toxicity, and variable exposure scenarios will improve predictions of population stability and inform adaptive management strategies.

CHAPTER 2: MODELING OF DISEASE TRANSMISSION IN LAKE TROUT (*SALVELINUS NAMAYCUSH*), LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) AND STEELHEAD TROUT (*ONCORHYNCHUS MYKISS*) POPULATIONS AND THE IMPACT OF PFAS EXPOSURE

1. INTRODUCTION

The Laurentian Great Lakes make up one fifth of the Earth's freshwater and provide habitat to several important tribal, recreational fisheries. (Morton, 2021; GLFC, 2024). Fish populations in the Great Lakes continue to be threatened by factors like climate change, invasive species entering the region and pollutants that are accumulating in these large water bodies (Alwin et al., 2024). Along with these anthropogenic issues challenging the Great Lakes, there are also infectious pathogens that can spread throughout fish populations and impact the health of valuable fisheries, of particular concern are the lake whitefish (*Coregonus clupeaformis*) infected with viral haemorrhagic septicaemia virus (VHSV), lake trout (*Salvelinus namaycus*) infected with epizootic epitheliotropic disease virus (EEDV) and steelhead trout (*Oncorhynchus mykiss*) species infected with *Flavobacterium psychrophilum*.

Over several decades, lake whitefish have been considered a valuable commercial fish species in the upper Great Lakes; however, their populations in certain areas of Lake Michigan and other Great Lakes have declined (Cunningham et al., 2023; Ebener et al., 2021). Between 2003 and 2012, the number of recruits per kg of spawners has declined by 76-80% in both Lake Michigan and Lake Huron (Ebener et al., 2021). Decreasing ice cover, the increasing presence of dreissenids, parasites and pathogens, like VHSV, have also played a part in the declining stocks found in the Lake Michigan main basin (Ebener, 2021).

In the early 1900s, VHSV caused a significant decline in farmed European rainbow trout populations and eventually began to impact fish in several states in the Pacific Northwest (Faisal et al., 2012). Infection from VHSV was first reported in whitefish in 1985 in Germany and Switzerland and has now been found in 82 different species around the world in both freshwater and marine environments (Skall et al., 2004; Cornwell et al., 2015). This virus is known to target the endothelial lining of blood vessels and fish that are infected with VHSV may experience necrotic degeneration of kidney, spleen, liver and intestinal tissues (Faisal et al., 2012). Transmission of VHSV mainly occurs horizontally from fish to fish and there is insufficient evidence to suggest vertical transmission from parent to offspring (Amos et al., 1998; Mohammadisefat et al., 2023).

Another Great Lakes fish that is important for both commercial and sport fishing, along with being a valuable native species and an apex predator, is lake trout (Shavalier, 2017, as cited in Redick, 1967 and Bronte et al., 2008). By the 1960s, lake trout populations faced serious declines in stock from overfishing and predation from invasive sea lamprey (Madenjian et al., 2023, as cited in Wells and McLain 1973, Holey et al. 1995, and Hansen 1999). To better manage this valuable fishery, a lake trout stocking program began in 1965 and continues to operate today (Madenjian et al., 2023, as cited in Holey et al., 1995, Madenjian et al., 2002 and LTWG, 2022). Although these stocking efforts began to help revive lake trout populations, infection with EEDV led to outbreaks among hatchery fish (Faisal et al., 2019). In the 1980s this virus infected millions of hatchery lake trout and led to the death of approximately 15 million juveniles across seven fish hatcheries in the Great Lakes region (Faisal & Loch, 2019). Fish infected with EEDV show signs of inappetence and lethargy and sometimes show skin lesions as well as hemorrhages in the mouth, eyes and fins (Genney et al., 2016a). Following infection from EEDV, young fish can experience mortality at high rates that can approach up to 100% (Bradley et al. 1989; McAllister and Herman 1989). Given the high rates or mortality among hatchery reared fish and younger age classes of fish, it is crucial to monitor the prevalence of EEDV among fish populations to try to prevent or limit damaging outbreaks. EEDV is primarily transmitted horizontally between fish although there is some evidence to suggest EEDV can also be transmitted vertically (Kurobe et al., 2009; Glenney et al., 2016a).

In response to the declining lake trout populations in the 1960s, stocking of salmonids like Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch)*, rainbow trout (*Oncorhynchus mykiss)* and brown trout (*Salmo trutta)* intensified in attempt to control alewife (*Alosa pseudoharengus*) populations and create a new sport fishery (Wegleitner et al., 2021, as citied in Mills et al., 1994, Dettmers et al., 2012). Since these stocking efforts in the 1960s, rainbow trout, also referred to as steelhead trout, have been consistently stocked into the Great Lakes and have economically benefitted many communities (Wegleitner et al., 2021, as cited in Dettmers et al., 2012). One concern for these hatchery steelhead populations is the pathogen, *F. psychrophilum,* which is the causative agent of bacterial coldwater disease (Bruce et al, 2020). This specific pathogen has caused major losses in hatchery populations of both trout and salmon and the cumulative mortality from outbreaks can be as high as 70%. There has been effort toward creating a vaccine for bacterial coldwater disease, but none has been approved for commercial use in the United States (Brenden et al., 2023). Not only can this pathogen be transmitted horizontally amongst fish, but there is also some evidence that suggests it may be transmitted vertically from parent to egg (Brown et al. 1997; Taylor 2004). This pathogen can cause necrotic lesions along with high rates of mortality among young fish through hemorrhagic septicaemia (Barnes and Brown, 2011; Duchaud et al. 2007). In rainbow trout, infections from this pathogen can cause mortality ranging from 3-30% when outbreaks occur (Wiens et al., 2018; Bruce et al., 2020).

When assessing the health and sustainability of the Great Lakes' most valuable fisheries, it is important to think about the pathogens that can threaten them, and what factors can cause these outbreaks to worsen. Fish are highly sensitive to changes in their environment and can become stressed when they experience conditions like low oxygen levels, poor water quality, changes in temperature and salinity (Pörtner & Peck, 2010, WorldFish, 2016). Environmental contaminants, such as PFAS, may also play a role in how pathogens spread throughout fish populations due to changes in immune and liver related gene function. Although the direct impact of PFAS contamination on parameters in infectious disease dynamics are not yet known, researchers have observed the down regulation of the interleukins (IL1β, IL6, IL8, IL11, and IL17D) along with some interleukin receptors which play a role in the regulation of inflammatory reactions and immune responses (Zhang et al., 2019). In another study done on striped bass in the Cape Fear River system, PFOS exposure was positively correlated with lysozyme and AST activity which also indicates some impact on liver and immune function (Guillette et al., 2020).

Given what is known about PFAS contamination and the impacts that exposure to these chemicals may play on the immune function of aquatic organisms, it is critical to start thinking about how the exposure to contaminants may play a role in the infection transmission, recovery and mortality experienced from infections. To begin investigating this topic, this chapter will model how specific pathogens are spreading throughout critical Great Lakes fish species. To do this, a SIR model (where S is susceptible, I is infected and R is recovered) was constructed for lake whitefish infected with VHSV, lake trout infected with EEDV and steelhead trout infected with *F. psychrophilum.* There is a lack of data surrounding how PFAS impacts the transmission, both vertically and horizontally, along with the recovery and mortality experienced from infection of these pathogens which makes modeling difficult although it is necessary. This is one of the first studies to simulate how PFAS-induced immunosuppression could alter pathogen dynamics in fish populations. In future simulations, the model parameters can be updated to include species specific effects from PFAS, but for this chapter, a sensitivity analysis will be conducted to see which model parameters have the largest impact on the infections and reproductive rates from these pathogens along with an example from preliminary data about how PFAS may impact this model. This will allow for hypotheses to be made about how PFAS might impact these parameters, and which parameters will show the largest impacts in real world populations. The objectives of this chapter are to 1) identify which parameters have the largest impact on the maximum proportion of infected individuals; 2) estimate the reproductive rate for each species based off data found in relevant literature; and 3) consider how PFAS may impact these model parameters and the spread of infectious pathogens throughout these populations.

2. METHODS

2.1. MODEL STRUCTURE

The structure of the SIR compartment model includes three main states: susceptible (S), infectious (I) and recovered (R) that describe the state of individual fish present in the population (Figure 2.1, Table 2.2, Equations T2.2.1-T2.2.3). This model was run under the assumption that pathogen transmission increased as the density of fish in a given area increased, otherwise known as density dependent transmission (Keeling and Rohani, 2008). The equations used in this model included several different parameters that impacted how fish transitioned from one state to the next (Figure 2.1, Table 2.2, Equations T2.2.1-T2.2.3). The natural mortality experienced from anything other than infectious pathogens remained constant throughout the model (μ). The parameter, β, known as the transmission coefficient was used to calculate how susceptible fish become infected at the rate of -βIS, where I is the density of infectious fish in the population at time t (Krkošek, 2010; Keeling and Rohani, 2008). The recovery rate, γ, was used to calculate how infectious individuals move to the recovered state where they are assumed to have lifelong immunity. The parameter, ρ, was incorporated to account for the deaths resulting from infection. Finally, the fixed birth rate, v, was used in the differential equation for susceptible fish to add new births into the population. This model assumes that once fish are infected, if they survive, they experience lifelong immunity and are not able to relapse and become infected again. It also assumes that the parameter values are not changing over time and remain constant throughout the course of the model.

Table 2.1 Parameters and symbols used in the SIR model.

Symbol	Description
S	Density of individuals susceptible to infection
I	Density of individuals infected by pathogen
R	Density of individuals that have recovered from infection
cv	Coefficient of variation
β	Transmission coefficient
N	Total population density
L	Average host lifespan
σ	Standard deviation
Ť	Recovery period (days)
μ(mean)	Mean
μ	Natural mortality rate
p	Probability of an infected individual dying from infection before recovery or dying from natural causes
γ	Recovery rate from infectious state
v	Fixed birth rate
R_0	Basic reproductive number
m	Per capita disease induced mortality rate for infected fish

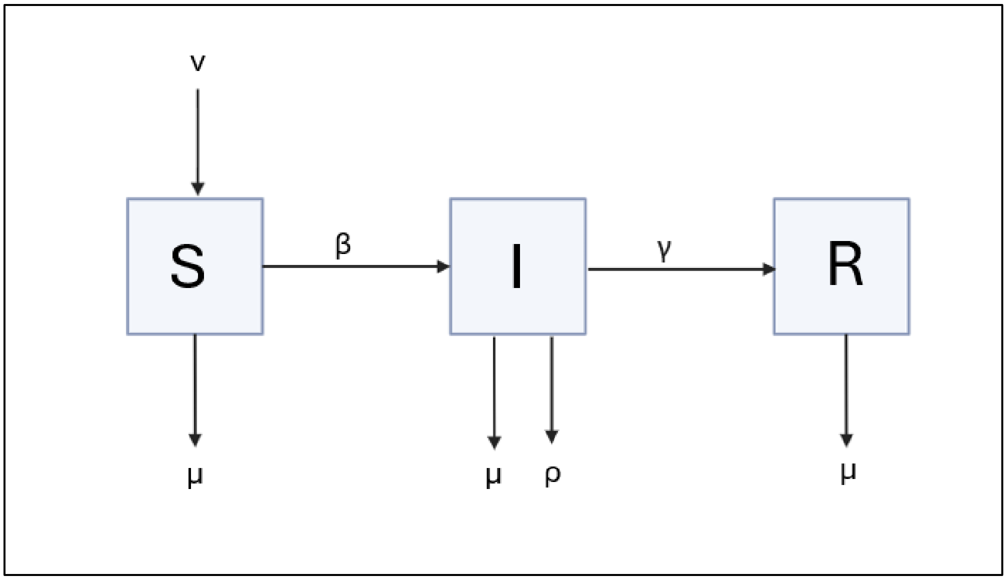

Figure 2.1 Compartmental structure of SIR model including vertical and horizontal transmission. The S, I and R boxes represent states of being susceptible, infectious or recovered from an infection. The rates on the arrows show how individuals move between each state. Created with biorender.com.

Table 2.2 Equations used for the SIR model.

Equations	
dS/dt = v - βSI - μS	(T2.2.1)
$\frac{dI}{dt} = \beta SI - \frac{(y+\mu)}{1-p} I$	(T2.2.2)
dR/dt = γI - μR	(T2.2.3)
$R_0 = \frac{\beta(1-p)v}{(\gamma+\mu)\mu}$	(T2.2.4)
γ = 1/T	(T2.2.5)
L = 1/μ	(T2.2.6)
$N \to \frac{v}{\mu}$	(T2.2.7)
$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right)$	(T2.2.8)
$N(t) = \frac{N_0 K}{(K - N_0)e^{-rt} + N_0}$	(T2.2.9)
$S = (1/R_0)$	(T2.2.10)
$cv = \frac{\sigma}{\mu(mean)}$	(T2.2.11)
$m = \frac{\rho}{1-\rho}(y+\mu)$	(T2.2.12)

A metric to determine if infectious pathogens will continue to spread throughout a population is defined as the basic reproductive ratio, R_o (Keeling and Rohani, 2008; Law et al., 2020; T2.2.4). R_0 is equal to the number of secondary infections that result from one index case in a population of susceptible fish. When $R_o > 1$, each infected individual on average will infect more than one other individual and the outbreak will continue to spread throughout the population. On the other hand, if $R_o < 1$, each individual will infect less than one other member of the population on average and the spread of infection within the population will eventually stop (Delamater et al., 2019).

The SIR model was simulated for each species over a period of 365 days. Model outputs comprise the densities (number of fish/ hectares of lake surface area) of susceptible, infected and recovered individuals. For data analysis, these densities were converted into the actual number of fish and then into proportions of the total population that fit into each state of S, I or R.

2.2. PARAMETER ESTIMATION

Average total population abundance of each species came from the MDNR stock assessment datasets (Newman et al., 2021, Turschak et al., 2021, and Lenart, 2024). For lake whitefish and lake trout, each management unit's population abundance was added together so that the SIR model would capture the dynamics occurring in Lake Michigan as a whole. Lake whitefish abundances were representative of ages 3+, while lake trout and steelhead were ages 1+. For the initial population densities, the average population levels between 1985-2022 for lake trout and 1986-2020 for lake whitefish were used. The approximate surface area needed to convert from population abundance to population density came from the 2017 Technical Fisheries Committee Administrative Report for lake trout and lake whitefish (Modeling Subcommittee, Technical Fisheries Committee. 2017). The total area was calculated by adding together the individual surface areas of all management units that were included in the total population count. For steelhead, since the population estimates were representative of the entire Lake Michigan, the surface area of approximately 5,757,300 hectares was initially used to calculate the density of fish/hectare (National Oceanic and Atmospheric Administration, 2024). Due to the small population size and large surface area of the steelhead trout data relative to lake whitefish and lake trout, an assumption was made that 80% of the surface area of Lake Michigan (4,605,840 ha) would be used to calculate the steelhead population density. This assumption was supported by a study looking at the catch rate data from steelhead fisheries to model the temporal and spatial distributions of steelhead trout (Höök et al., 2004). This study found that throughout the course of the year, portions of Lake Michigan showed no detections related to catch per unit effort (CPUE) meaning that no fish were being caught in these regions. As weather and temperature changed throughout the year, these areas with no CPUE data fluctuated, but were still observed in each month that was mapped (May, June, July, August, and September).

The data needed to find the recovery rate, γ, were the average length of an infectious period (Keeling and Rohani, 2008; Olson, 2013; Faisal et al., 2019; Brenden et al., 2023; T2.2.5). The inverse of the average lifespan of each species was used to solve for μ, the natural mortality rate (Maine Dept of Inland Fisheries and Wildlife, 2024; Michigan Department of Natural Resource, n.d., *Lake Trout*; Michigan Department of Natural Resource, n.d., *Steelhead;* T2.2.6). Equation T2.2.7 was used to find the fixed birth rate, v, where N is approximately equal to the concept of carrying capacity for each population (Keeling and Rohani, 2008). To find the carrying capacity for each population, the solution to the logistic growth equation was used to estimate population growth between 1985-2022 for lake trout, 1986-2020 for lake whitefish and 1985-2021 for steelhead trout (T2.2.8; T2.2.9). The sum of squares was then calculated, and

Microsoft Excel's solver was used to minimize the sum of squares by changing r, the growth rate and K, the value for carrying capacity. Finally, to find β, the equation for the basic reproductive ratio, R_0, was rearranged and the other parameter values were used to calculate beta (T2.2.4). R_0 for each species was estimated using studies looking at the prevalence of each specific pathogen in wild populations of freshwater fish through qRT-PCR, qPCR and PCR assays (T2.2.10; Thiel et al., 2020; Cornwell et al., 2015; Glenney et al., 2016a; Ekman et al., 1999; Van Vliet et al., 2015). For this calculation, any fish that did not test positive for the pathogen was considered a 'susceptible'.

Table 2.3 SIR model simulation parameter values for each of the model species along with the calculations for each species' R_0 value.

Species	β	γ	μ	v	p	Proportion of Initial Infections	R_0
Lake Whitefish	0.00674	0.04762	0.00011	0.00090	0.00952	0.134	1.154736
Lake Trout	0.02329	0.02198	0.00014	0.00015	0.00595	0.135	1.156121
Steelhead Trout	0.17972	0.04167	0.00055	0.00015	0.01400	0.106	1.118214

The proportion of initially infected fish for each species was identified from studies where wild fish were captured and sampled for pathogen detection. For lake trout, across nine different water bodies, 6 of them contained fish that tested positive for EEDV. Across all 9 water bodies, a total of 548 fish were sampled with a total of 208 fish being tested from the sites that showed positive results for EEDV. Seventy-four of the 208 fish from these areas tested positive through a TaqMan qPCR assay or SYBR Green qPCR, which is equal to roughly 13.5% of the total number of fish sampled (Glenney et al., 2016a). Lake whitefish started with 13.4% of the population being considered infected. This was derived from two studies where fish were collected from different sites within the Great Lakes' region. In one study, multiple fish species were sampled and of the 5090 collected, 13% tested positive for VHSV via qRT-PCR or virus isolation in cell culture (Cornwell et al., 2015). In the other study, Fish were captured via fyke netting, boom shocking, stream shocking or spawning weir across 46 different inland water bodies. OF all 1,697 fish that were sampled, 14.6% of them tested positive for VHSV antibodies (Thiel et al., 2021). The initial portion of infected steelhead also came from two different studies. The first was looking for *F. psychrophilum* in Baltic salmon where they were caught during their spawning migration and *F. psychrophilum* was isolated from 7/50 or about 14% of fish sampled (Ekman et al, 1999). The second study found that 30/300 or 10% of the steelheads they sampled from Lake Michigan were found to be infected with *F. psychrophilum*. (Van Vliet et al., 2015).

To find the number of fish that died throughout the course of the simulation, the per capita disease mortality rate of infectious fish, m, was calculated using equation T2.2.12 (Keeling and Rohani, 2008). This mortality rate was then multiplied by the density of infected fish at each timestep to find the approximate density of fish that were dying after becoming infected. This density was then multiplied by the total area that each species covered in Lake Michigan to find the actual number of fish that died rather than the number of fish per hectare.

2.3. SIMULATIONS

To investigate the initial conditions present for each pathogen in its respective host, baseline simulations were run using the average population density from MDNR datasets as the starting value for N; this will be referred to as the "real density simulations". Along with this baseline simulation, two other PFAS free simulations were run for each species: one where the population density (fish/hectare) was doubled from the baseline conditions to see how the dynamics would change when there were more fish in a given area ("doubled density simulations"), and one where all three species experienced the same levels of population density and the initial proportion of infected individuals ("same density simulations"). For the simulations that used the same density and proportion of initially infected fish, the values used came from averaging all three species together (N= 2.9396 fish/hectare and 12.6% initially infected fish).

To analyze what impact PFAS might have on this model, two more simulations were run for each species under the real density and doubled density conditions: one where ρ was increased, and one where γ was decreased, along with increases to ρ and β. These parameter changes were based on the findings of an unpublished pilot study by Adrian Deil Manliclic, where lake trout were exposed to EEDV, and one treatment group was exposed to both PFOS and EEDV. Dissections occurred throughout the experiment and samples were taken from the eyes, skin and fin to test for EEDV. The results of this preliminary study showed that by day 21, the fish exposed to both EEDV and PFOS carried 3,632,82.5 copies of the virus per mg of tissue sampled compared to the EEDV only fish which carried 834,813.4 copies per mg (these values were averaged across all three tissue samples and fish collected for each treatment). By day 28, the PFOS/EEDV group contained 2,480,872.7 copies per mg while the EEDV only group had 1,107,472.8 copies per mg. Manliclic also found that the PFOS treated group showed two mortalities, one on day 16 and the other on day 22 (Unpublished). The control and EEDV only groups did not show any mortalities throughout the course of the 28-day experiment. This increase in the viral copies per mg of the PFOS exposed fish along with the increased number of mortalities within this group suggest that PFOS exposure might influence how fish are responding to pathogens (Manliclic, Unpublished). After this preliminary study was completed, the full experiment was conducted over 56 days where lake trout were once again exposed to PFOS and EEDV. At this point, the only data available from this full 56-day study is mortality data as the eye, skin and fin samples have not yet been analyzed. The control and PFOS only groups showed no mortalities, the EEDV-only group had 5 deaths and the PFOS/EEDV treatment group had 10 deaths. The mortality in the PFOS/EEDV groups showed a 100% increase from the mortality found in the EEDV only group (Manliclic, Unpublished).

The 100% increase in mortalities found in the unpublished disease challenge experiment was used to justify doubling the parameter, ρ. Based on available literature about how PFAS may impact immune function along with the preliminary results of the disease challenge experiment showing higher copies of EEDV/mg after PFOS exposure, an assumption was made that the recovery rate would decrease by 20% and the transmission coefficient would increase by 20%. This 20 percent value was arbitrarily selected due to a lack of data about how these individual parameters are precisely impacted by PFOS.

2.4. SENSITIVITY ANALYSIS

To determine which parameters had the largest influence on the maximum proportion of infected individuals over the 365 days, a sensitivity analysis was conducted. The parameters that were tested in the sensitivity analysis were the recovery rate, γ, transmission coefficient, β, death rate, μ, and disease mortality rate, ρ and the fixed birth rate, v. The only parameter that was not chosen for the sensitivity analysis was the density of fish considered to be recovered from the start, because for these simulations, it was assumed to be 0. This analysis was conducted using three different coefficients of variations, 1%, 10% and 25%. To generate the data used for each specific coefficient of variation, the parameter values from the simulations were used as the mean parameter values and the standard deviations for each parameter were calculated using either a 1%, 10% or 25% CV (T2.2.11).

For each parameter, at each level of variation, n=100 different datapoints were generated using the Latin Hypercube Sampling (LHS) method and were picked from a normal distribution to ensure that the distribution of data points was evenly distributed over the given domain for the samples to show true variability (Ivan, 2018). In this method of sampling, one hypercube contains one sample in each coordinate axis and it remembers the previous samples when choosing the next one. These sensitivity analyses illustrate how much each of the parameters impact the maximum proportion of infected fish throughout the course of a year.

3. RESULTS

3.1. LAKE WHITEFISH

The lake whitefish baseline simulations showed that the maximum proportion of infected fish was equal to the starting proportion of infections and tapered out throughout the course of the model. On day 365, only 0.0001 (0.01%) of the population was still considered to be infectious, while 44.99% recovered and 55.0% remained susceptible (Figure 2.2a). When the PFOS effects were added, the highest proportion of infected individuals went up to 0.1619 (16.19%), however, by the end of the 365-day simulation the infection also tapered out with only 0.035% of the population still being infected while 69.1% of the population had reached the recovered state and 30.85% remained susceptible (Figure 2.2b).

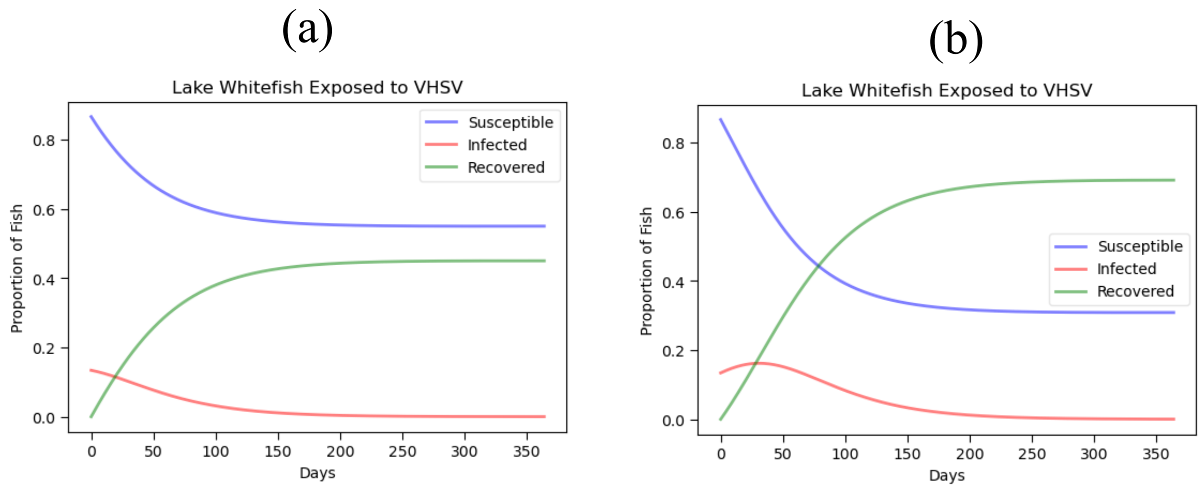

Figure 2.2 SIR model simulations of the course of 365 days using the real population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Lake whitefish were exposed to VHSV using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

In the simulations where the initial population density was doubled, the maximum percentage of infected fish was 23.39% for the PFOS-free simulation compared to 35.89% when PFOS effects were included. The percentage of susceptible fish remaining in the population also decreased following exposure to PFOS while the percentage of fish that recovered from the infection went from 84.41% in the PFOS-free simulation to 95.02% in the PFOS-exposed simulation (Figure 2.3).

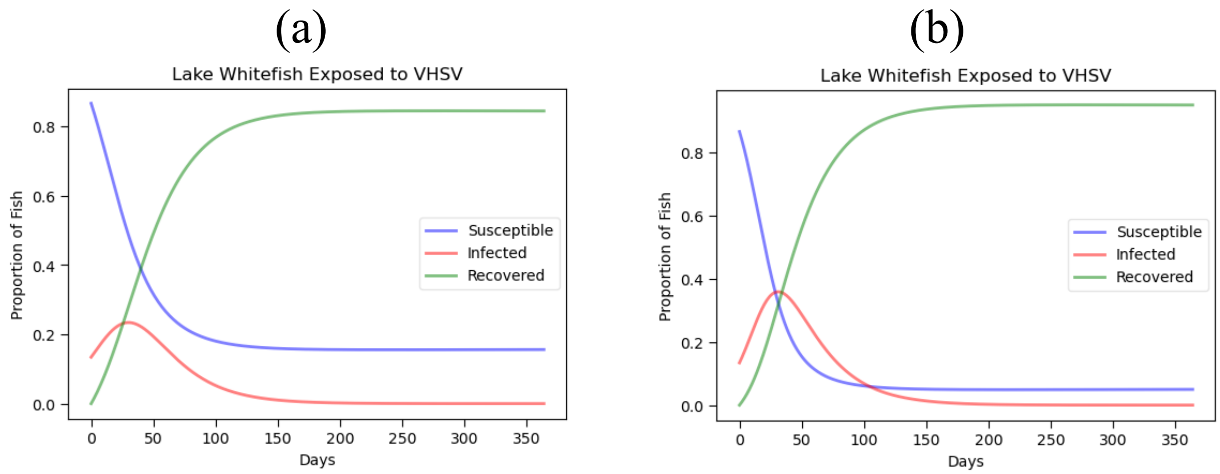

Figure 2.3 SIR model simulations of the course of 365 days using the doubled population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Lake whitefish were exposed to VHSV using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

The sensitivity analysis found that the most sensitive parameters in terms of the maximum proportion of infected fish were the starting population density and the initial density of infected fish (Table 2.4). The recovery rate parameter in the 25% CV simulation also showed an R^2 value of 0.1853 or 18.53%. The parameters with an R^2 values above 0.2 or 20% for the proportion of recovered fish on day 265 were the recovery rate, transmission coefficient and initial density of infected fish. The population density parameter also showed an R^2 value of 0.1642 for the 1% CV simulation and 0.1573 for the 10% CV simulation.

Table 2.4 Lake whitefish percent variance (R^2) between SIR model parameters and maximum proportion of infected individuals along with the remaining proportion of recovered fish on day 365 of the simulation. Parameters were generated using 1%, 10% and 25% coefficients of variation. The bolded values show the highest R^2 values greater than 20% and the underlined values showed R^2 values between 10-20%.

Lake Whitefish						
Parameters	1% CV	10% CV	25% CV	1% CV	10% CV	25% CV
	Maximum Proportion of Infectious Fish			Proportion of Recovered Fish on Day 365		
Natural Mortality Rate (μ)	0.0003	0.0002	0.0087	0.0064	0.0010	0.0044
Birth Rate (ν)	0.0196	0.0146	0.0135	0.0010	0.0114	0.0005
Recovery Rate (γ)	0.0001	0.0016	<u>0.1853</u>	<u>0.1961</u>	**0.3064**	**0.4782**
Transmission Coefficient (β)	0.0082	0.0148	0.0568	**0.4739**	**0.4064**	**0.3088**
Probability of Disease Mortality (ρ)	0.0019	0.0054	0.0163	0.0040	0.0092	0.0345
Population Density (N)	**0.4583**	**0.5179**	<u>0.1945</u>	<u>0.1642</u>	<u>0.1573</u>	0.0314
Initial Infected Density (Y0)	**0.4623**	**0.5218**	**0.4534**	**0.2115**	0.0501	<u>0.1287</u>

3.2. LAKE TROUT

The lake trout baseline simulations showed a maximum proportion of infected fish of 0.1389 which increased slightly from the day 0 proportion of infected fish which was 0.135 (13.5%) and then began decreasing until day 365 where only 1.11% of fish remained infected. When PFOS effects were simulated, the maximum percentage of infected fish rose to 21.29% and around 2.09% of the fish remained infected on day 365. By the end of the 365 days, the baseline simulations showed 55.4% of the population recovered compared to the PFOS simulation where 76.59% of the population had already recovered from infection (Figure 2.4).

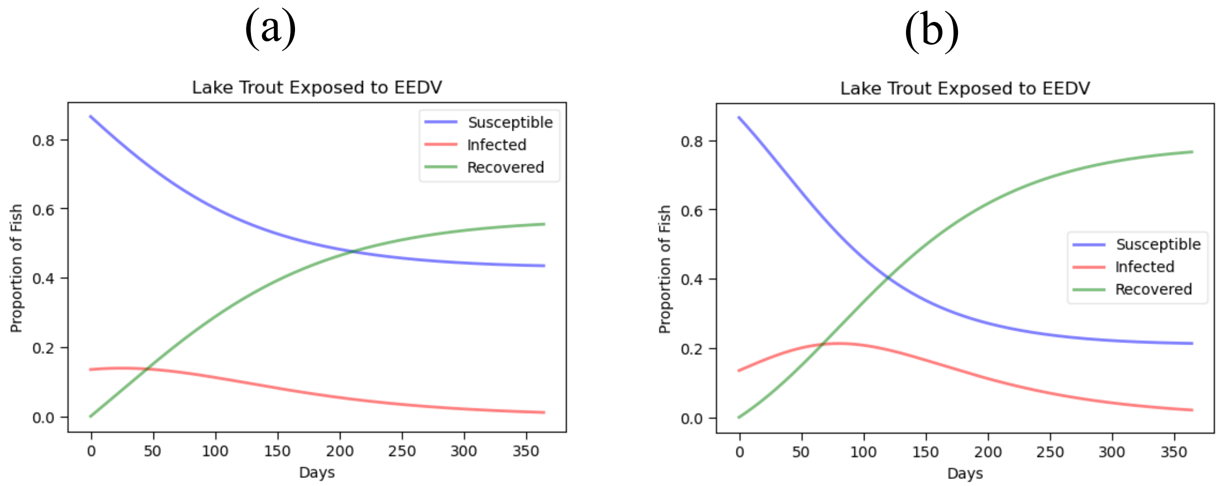

Figure 2.4 SIR model simulations of the course of 365 days using the real population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Lake trout were exposed to EEDV using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

When population density was doubled, the maximum percentage of infected fish was 29.97% in the control population and 42.84% in the PFOS-exposed population. By the end of the 365 day simulation, the PFOS-exposed population had a 6.19% higher maximum percentage of recovered fish in the population, although both simulations resulted in over 90% of the population ending up recovered from the infection (Figure 2.5).

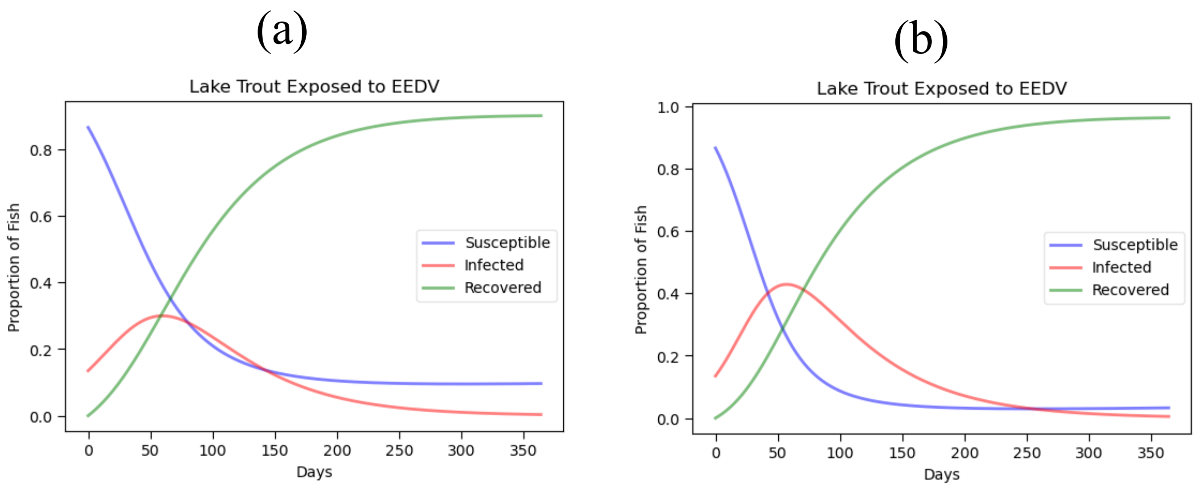

Figure 2.5 SIR model simulations of the course of 365 days using the doubled population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Lake trout were exposed to EEDV using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

The sensitivity analysis found that the parameters with R^2 values greater than 0.2 or 20% for the maximum proportion of infected fish were the recovery rate, transmission coefficient and the initial density of infected fish. The probability of disease mortality also had an R^2 value of 0.1063 or 10.63%. For the proportion of recovered fish on day 365, the most sensitive parameters with R^2 values over 0.2 were the recovery rate, transmission coefficient and the population density (Table 2.5).

Table 2.5 Lake trout percent variance (R^2) between SIR model parameters and maximum proportion of infected individuals from an uncertainty analysis where parameters were generated using 1%, 10% and 25% coefficients of variation. The bolded values show the highest R^2 values greater than 20% and the underlined values showed R^2 values between 10-20%.

Lake Trout

Parameters	1% CV	10% CV	25% CV	1% CV	10% CV	25% CV
	Maximum Proportion of Infectious Fish			Proportion of Recovered Fish on Day 365		
Natural Mortality Rate (μ)	0.0001	0.0011	0.0145	0.0003	0.0001	0.0102
Birth Rate (v)	0.0001	0.0096	0.0000	0.0000	0.0107	0.0036
Recovery Rate (γ)	0.1481	**0.3401**	**0.2289**	**0.3933**	**0.3259**	**0.3157**
Transmission Coefficient (β)	0.1568	0.0767	**0.2173**	**0.3122**	**0.4583**	**0.5124**
Probability of Disease Mortality (ρ)	0.1063	0.0066	0.0000	0.0171	0.0059	0.0159
Population Density (N)	0.0625	0.0958	0.0049	0.1987	0.0871	**0.2410**
Initial Infected Density (Y0)	**0.5969**	**0.3438**	0.0048	0.0312	0.0485	0.0019

3.3. STEELHEAD TROUT

Similar to lake trout and lake whitefish, the maximum percentage of infected fish increased with PFOS exposure for steelhead populations (12.09% to 21.87%). The maximum percentage of recovered fish also increased from 55.44% to 76.5%. Both simulations showed less than 2.1% of fish in the infectious state by day 365 of the simulation (Figure 2.6).

(a) (b)

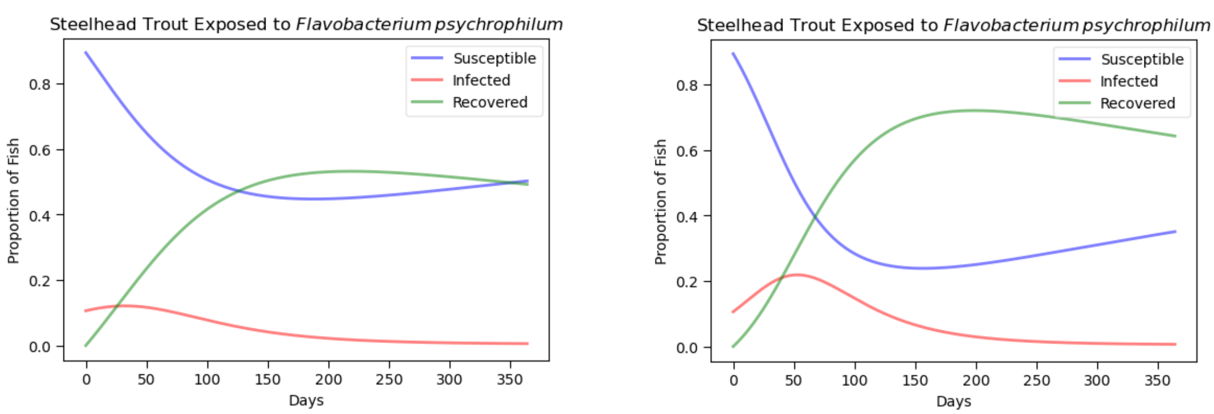

Figure 2.6 SIR model simulations of the course of 365 days using the real population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Steelhead trout were exposed to *F. psychrophilum* using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

When densities were doubled, the maximum percentage of infected fish went from 31.40% in the baseline population to 44.65% when PFOS effects were added. The maximum percentage of fish that reached recovery was 86.14% for the baseline simulations compared to 90.82% for the PFOS simulation. Both simulations resulted in less than 1% of fish remaining infected by the end of the year (Figure 2.7).

(a) (b)

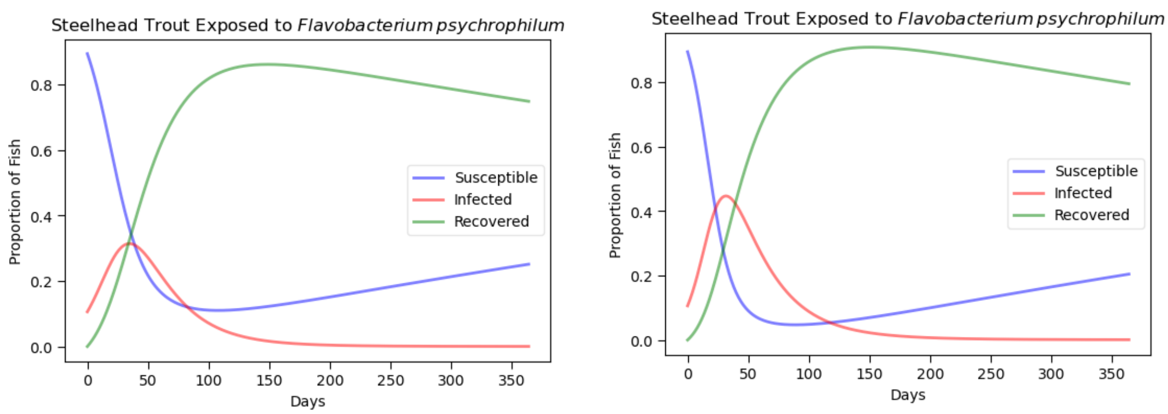

Figure 2.7 SIR model simulations of the course of 365 days using the doubled population densities from abundance and surface area estimates for Lake Michigan. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. Steelhead trout were exposed to *F. psychrophilum* using (a) baseline conditions and (b) PFOS effects added to γ, β, and ρ.

The sensitivity analysis for the maximum proportion of infectious fish resulted in the recovery rate, transmission coefficient and population density were the parameters with the highest R^2 values greater than 20%. The initial density of infected fish also showed an R^2 value of 0.1424 or 14.24%. The most sensitive parameters for the proportion of recovered fish on the final day of the simulation were also the recovery rate, transmission coefficient and the population density (Table 2.6).

Table 2.6 Steelhead trout percent variance (R^2) between SIR model parameters and maximum proportion of infected individuals from an uncertainty analysis where parameters were generated using 1%, 10% and 25% coefficients of variation. The bolded values show the highest R^2 values greater than 20% and the underlined values showed R^2 values between 10-20%.

Steelhead Trout

Parameters	1% CV	10% CV	25% CV	1% CV	10% CV	25% CV
	Maximum Proportion of Infectious Fish			Proportion of Recovered Fish on Day 365		
Natural Mortality Rate (μ)	0.0077	0.0021	0.0221	0.0421	0.0489	0.0009
Birth Rate (v)	0.0249	0.0087	0.0717	0.0282	0.0283	0.0306
Recovery Rate (γ)	**0.3851**	**0.3536**	**0.4541**	**0.4568**	**0.5853**	**0.3922**
Transmission Coefficient (β)	**0.3313**	**0.4043**	**0.2244**	**0.3370**	**0.4348**	**0.4618**
Probability of Disease Mortality (ρ)	0.0001	0.0032	0.0076	0.0019	0.0319	0.0002
Population Density (N)	**0.2602**	0.0092	0.0014	**0.2524**	<u>0.1060</u>	<u>0.1204</u>
Initial Infected Density (Y0)	<u>0.1424</u>	0.0874	0.0275	0.0068	0.0004	0.0050

3.4. COMPARISON

When the “same density” simulations were run using the average population density and percentage of initially infected fish from all three species, steelhead trout showed the highest maximum proportion of infected fish and recovered fish (Figure 2.8). Lake whitefish showed the lowest levels of infection and the highest proportion of fish remaining susceptible throughout the simulation.

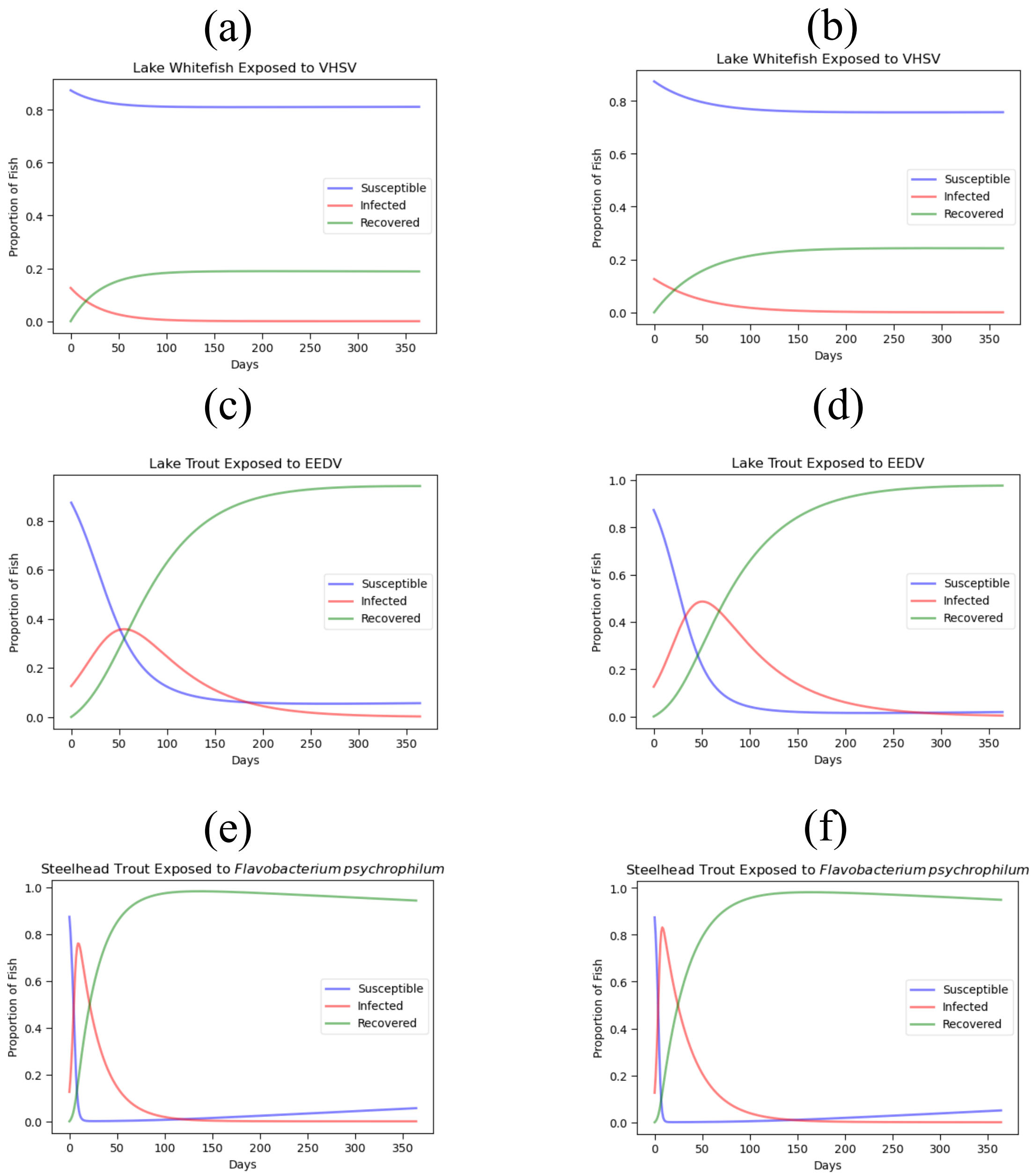

Figure 2.8 SIR model simulations of the course of 365 days using the same average population densities from abundance and surface area estimates for Lake Michigan for all three species. The x axis covers the number of days and the y axis is the proportion of fish in the population that are in each state of S,I or R. (a), (b) and (c) show the three different species using with no PFOS effects included, while (d), (e), and (f) show the PFOS exposures. (a) and (d) show the plots for lake whitefish exposed to VHSV, (b) and (e) show lake trout exposed to EEDV and (c) and (f) show steelhead trout exposed to *F. psychrophilum.*

Across all three species from the “real density” PFOS simulations, lake trout and steelhead trout both showed over 21% of their populations reaching the infectious state throughout the 365 days. The maximum percentage of infected fish in the lake whitefish simulation reached 16.2% (Table 2.7). In the PFOS-free, “real density” simulations, lake trout showed the highest maximum percentage of recovered fish throughout the simulation (55.44%) compared to lake whitefish (45.0%) and steelhead trout (53.20%). When the population densities were doubled, steelhead showed the highest percentage of infectious fish (31.40%) followed by lake trout (29.97%) and lake whitefish (23.39%). When the same density and proportion of initially infected fish were used for all three species, steelhead trout showed significantly hi gher proportions of infected fish within the first 50 days of the simulation and then the infectious fish quickly declined to reach 0.0000091 or (0.00091%) by day 365 of the simulation (Figure 2.8e; Figure 2.8f). This same trend occurred when PFOS effects were added into the simulation with steelhead reaching a maximum proportion of infected fish (83.13%) before day 50 of the simulation. In the “same density” simulations both including and excluding the effects from PFOS, lake whitefish showed the lowest proportions of infected fish and infection rates declined from day 1 of the simulation, ultimately reaching <0.01% of the population by day 365 (Figure 2.8a; Figure 2.8b). Lake whitefish also showed the lowest proportions of recovered fish throughout the simulation and the highest proportion of fish remaining susceptible to infection.

Table 2.7 Model outputs of the maximum proportion of infected fish, maximum proportion of recovered fish along with day 365 values for the proportion of susceptible, infected and recovered fish for all three species from all SIR simulations. All proportions in this data table are between 0 and 1 and when multiplied by 100 represent the percentage of the total population.

Species	Simulation	R_0	Max Proportion of Infected Fish	Max Proportion of Recovered Fish	S_{365}	I_{365}	R_{365}
Lake Whitefish	Real Density	1.15474	0.134000	0.449961	0.549958	0.0001	0.4499416
	Real Density PFOS	1.71446	0.161891	0.691151	0.3085	0.0003495	0.6911508
	Double Density	1.15474	0.233942	0.844442	0.155935	7.31E-06	0.8440577
	Double Density PFOS	1.71446	0.358859	0.950668	0.049783	9.27E-06	0.9502079
	Same Density	1.15474	0.126000	0.189390	0.811521	8.47E-07	0.1884782
	Same Density PFOS	1.71446	0.126000	0.242742	0.757479	5.90E-05	0.2424624
Lake Trout	Real Density	1.15612	0.138862	0.554402	0.434526	0.011072	0.5544017
	Real Density PFOS	1.72113	0.212942	0.765918	0.21321	0.0208722	0.7659183
	Double Density	1.15612	0.299704	0.900088	0.0965	0.0034127	0.9000876
	Double Density PFOS	1.72113	0.428404	0.961963	0.032826	0.005211	0.9619634
	Same Density	1.15612	0.358108	0.941687	0.056243	0.0020695	0.9416872
	Same Density PFOS	1.72113	0.486549	0.977279	0.018849	0.0038722	0.9772792
Steelhead Trout	Real Density	1.11821	0.120896	0.531960	0.502406	0.0056204	0.4919738
	Real Density PFOS	1.64815	0.218732	0.720439	0.350584	0.0066628	0.6427536
	Double Density	1.11821	0.313994	0.861370	0.251149	0.0002075	0.7486436
	Double Density PFOS	1.64815	0.446591	0.908184	0.204249	0.000853	0.794898
	Same Density	1.11821	0.760331	0.983327	0.056357	9.91E-06	0.9436326
	Same Density PFOS	1.64815	0.831346	0.981603	0.050628	0.0001742	0.9491976

In the real density simulations, the effects of PFOS exposure caused the largest percent change from the baseline conditions in steelhead trout (80.9%), followed by lake trout (53.3%) and lake whitefish (20.8%) (Figure 2.9). The simulation where the population density per hectare was doubled, lake whitefish showed the largest percent change (53.4%), followed by lake trout

(42.9%) and steelhead trout (42.2%). Finally, in the same density simulation, lake whitefish did not show any change in the maximum proportion of infected fish while lake trout showed a 35.9% increase and steelhead trout showed a 9.3% increase (Figure 2.9).

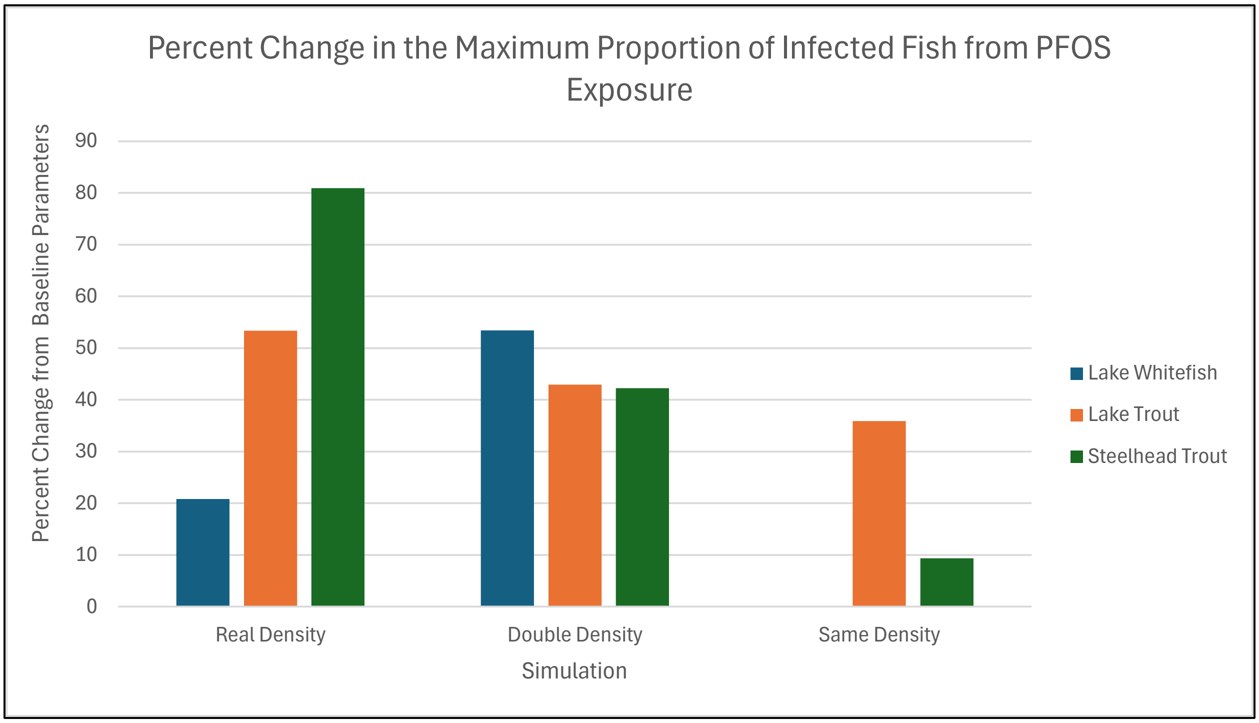

Figure 2.9 Percent change in the maximum proportion of infected fish throughout the 365-day simulation for lake trout, lake whitefish and steelhead trout that were exposed to PFOS effects. These percent changes are shown for the three different simulations where different starting densities of fish were used as model inputs.

The simulation resulting in the largest number of lake whitefish deaths was the “double density” PFOS exposure (Table 2.8). For lake trout and steelhead trout, the largest number of deaths resulted from the “same density” PFOS exposure. The largest percentage change from exposure to PFOS effects for all three species was found in the “real density” simulations where deaths increased by 208.1% for lake whitefish, 176.6% in lake trout and 163.8% in steelhead trout.

Table 2.8 Number of fish deaths resulting from the infection of a specific pathogen for all six simulations. Lake whitefish were exposed to VHSV, lake trout were exposed to EEDV, and steelhead trout were exposed to *Flavobacterium psychrophilum.*

Species	Simulation	Deaths
Lake Whitefish	Real Density	57,100.2
	Real Density PFOS	175,935.5
	Double Density	213,663.0
	Double Density PFOS	481,611.6
	Same Density	9,699.4
	Same Density PFOS	25,242.1
Lake Trout	Real Density	12,270.8
	Real Density PFOS	33,935.6
	Double Density	39,103.0
	Double Density PFOS	83,730.8
	Same Density	49,444.2
	Same Density PFOS	102,794.9
Steelhead Trout	Real Density	16,669.5
	Real Density PFOS	43,973.9
	Double Density	41,325.3
	Double Density PFOS	88,239.0
	Same Density	191,953.6
	Same Density PFOS	386,607.7

The sensitivity results of all lake trout and steelhead trout showed that for the maximum proportion of infected fish, the recovery rate and the transmission coefficient were two of the most sensitive parameters with R^2 values greater than 0.2. Lake Whitefish and steelhead trout showed that population density was one of the most sensitive parameters, while lake whitefish and lake trout found the initial density of infected fish to be one of the most sensitive parameters.

All three species showed that the recovery rate and the transmission coefficient were two of the most sensitive parameters for the proportion of recovered fish on day 365 (Tables 2.4-2.6).

4. DISCUSSION

The "real density" simulations showed that steelhead trout had the largest percent change in the maximum proportion of infectious fish compared to the other two species. This finding was likely the result of the increase in the transmission coefficient, β. The baseline value for beta is much higher for steelhead trout (0.17972) compared to lake trout (0.02329) and lake whitefish (0.00674), so when there was a 20% increase but no change to population density, more fish were able to contract the infection. The sensitivity analysis for the maximum proportion of infected fish also confirmed that the transmission coefficient was one of the most sensitive parameters for steelhead trout, whereas the transmission coefficient for lake trout and lake whitefish had lower sensitivity. Lake trout showed the second largest percent change in the "real density" simulations; the baseline data for lake trout showed that lake trout had the lowest recovery rate compared to the other two species and when PFOS exposure caused this rate to decline more, a higher proportion of fish were able to stay in the infectious class per timestep. Lake whitefish showed the lowest percent change while having the highest recovery rate and the lowest transmission coefficient of all three species.

Across all three species, when their original population densities were doubled, there were higher proportions on infected individuals and lower proportions of fish ending in the susceptible group. Between all three species, lake whitefish had the highest density of fish per hectare and when these densities were doubled, lake whitefish started with a much higher density of fish in the simulation than the other two species, likely leading to the increased percent change in the proportion of infected fish in the population. Lake whitefish also showed the highest sensitivity (highest R^2 values) for the population density parameter, N, across all three coefficients of variation in the sensitivity analysis. This finding of increased proportions of infected and recovered fish due to increases in population density were supported by several different mass mortality events in hatchery fish populations that are held in higher densities than fish in Lake Michigan. For example, in hatchery stocks, EEDV exposure has historically caused major losses to lake trout; in the 1980s, these losses reached approximately 15 million juveniles across seven state and federal fish hatcheries in the Great Lakes region (Faisal et al., 2019). This virus has also caused major mortality events amongst hatchery fish populations in 2012, with a loss of approximately 100,000 fish and in 2017, with similar mortality rates to 2012 (Shavalier, 2017).

The last simulation where all three species used the same average densities and proportion of initially infected fish in their simulations showed that lake whitefish had no change between the baseline conditions and the simulations where PFOS effects were added. Given the high density of fish per hectare in the real populations in Lake Michigan, when this was reduced to the average value of 2.9396, the contact between fish was much lower than the real conditions, which caused the infectious fish to decline after day 1 of the simulation. The opposite trend occurred in the steelhead population where the value of the population density was 2.6506 fish/hectare larger than the density in the real population. This substantial increase in the number of fish in each hectare of Lake Michigan caused the infectious individuals to rapidly increase after day 1 of the simulation and over 94% of the population to have reached the recovered state before day 365. When PFOS effects were included in the “same density” simulations, both lake trout and steelhead trout showed increases in the proportion of fish becoming infected with their respective pathogens.

All three fish species showed the largest percentage increase in the number of deaths from PFOS exposure in the “real density” simulations. All three species also showed over 100% increases in the number of deaths when the effects of PFOS were added in all three simulations. These drastic increases in disease mortality highlight the threat that exposure to contaminants like PFOS may pose on species already threatened by infectious pathogens. The mortality data also highlights that when species are living in higher densities, more fish become infected and larger numbers end up dying, while exposure to PFOS exacerbates this even further (Anderson and May, 1991; Hudson et al. 2002, as cited in Krkosek, 2010).

4.1 LIMITATIONS

One of the key limitations for this model was that once a fish became infected, it either recovered, stayed in the infected group, or died from infection or natural causes rather than becoming reinfected or carrying the pathogen and potentially exposing other fish. If fish were able to become reinfected or carry the virus without showing signs of infection while spreading it to other fish as shown in Skall et al. (2004) and Shavalier et al. (2020), the impacts of PFOS exposure on the transmission of these pathogens may be even greater and lead to higher proportions of fish dying from these diseases.

Although demography was included in this model and it was assumed that there were births and deaths entering and exiting the population, the starting population density was assuming that the total population abundance of fish within a given area were evenly distributed per hectare of surface area. Fish are not sedentary creatures and are usually moving throughout waterbodies; their locations are dependent on a wide range of conditions like bottom type, turbidity, oxygen concentrations, temperature, interspecific interactions, and density-dependent processes (Planque et al., 2010). Habitat suitability models in Michigan river systems showed that total fish density among different sites ranged from 5-1004 pounds per acre; this result captured the varying nature of fish density at different locations within a large waterbody (Zorn et al., 2009). The model also assumed uniform PFAS exposure across populations, but PFAS contamination in real lakes is highly spatially heterogeneous.

Another model limitation was the assumption that vertical transmission was negligible and was not adding any new fish to the infected state, all new births were being added to the susceptible state. Although transmission is primarily transmitted horizontally between fish, there is some evidence to suggest EEDV can also be transmitted vertically (Kurobe et al., 2009; Glenney et al., 2016a). Regarding *F. psychrophilum,* there is also some evidence that suggests it may be able to transmit vertically from the female parent to egg (Brown et al. 1997; Taylor 2004). VHSV on the other hand has insufficient evidence to suggest vertical transmission from parent to offspring (Amos et al., 1998; Mohammadisefat et al., 2023).

The dynamics in this simulation were also impacted by the way that β was calculated using pathogen detection data from wild fish populations. Ideally, to be more accurate with the estimate of beta, R_0 could be estimated using data about reported cases (Keeling and Rohani, 2008). This method is typically used in cases where there were high levels of reporting for infections in a given time. The data about the number of infections in a given period could also be used to estimate the transmission coefficient using the methods discussed in Lounis and Bagal (2020). Due to the lack of consistent infection data for all three species available from literature, this method would have likely underestimated or misrepresented the value of R_0 and β. Another alternative was to use age specific seroprevalence data, but once again, for these specific species and pathogens, there was not enough literature looking into seropositivity across different age classes (Keeling and Rohani, 2008).

In future work, this model could be adapted to include an exposed stage to capture the latent period where fish are exposed to pathogens but not yet considered infectious (Girardi and Gaetan, 2021). In lake trout, the incubation period of EEDV is between 9-18 days for water borne exposures done at 9 ± 1 degrees Celsius (Shavalier et al., 2020). The input data for the parameter, ρ, could also be modified based on the species-specific findings in the ongoing disease challenge experiments by Manliclic. This model assumed that the 100% increase in the mortality experienced by lake trout infected with EEDV applied to lake whitefish infected with VHSV and steelhead trout infected with *F. psychrophilum,* when the mortality from infection may be different between different species and pathogens.

Future adaptations of this model may also include the effects from different PFAS compounds besides PFOS, the impacts of different exposure levels throughout the population, and the impact of mixtures and other stressors in combination with PFAS exposure. By only modeling effects of one PFAS compound, the impact on pathogen transmission, mortality and recovery may be underestimated.

4.2 IMPLICATIONS FOR MANAGEMENT

This model is the first step toward simulating and better understanding how impacts on immune function caused by PFAS contamination may impact the spread of disease throughout valuable fish populations. One of the most important preventative measures for limiting the spread of pathogens is to reduce risk factors like poor water quality and stress, so it is crucial to understand the impact that PFAS have on vulnerable populations to more effectively manage the spread of disease (Shoemaker et al., 2015). Future versions of this model can be adapted to investigate how other contaminants or stressors impact pathogen transmission and mortality amongst fish or wildlife of concern. As more information comes to light about how different

PFAS compounds impact these species and the spread of pathogens throughout their populations, the input data for this model can be updated to reflect these discoveries.

Overall, this model can be used as a tool to assess the presence and spread of infections throughout fish populations, and how PFAS exposure may be worsening these outbreaks through increased rates of transmission, higher rates of mortality and prolonged recovery times following infection. It may also help to inform management decisions such as implementing targeted disease monitoring in PFAS hotspots or testing for contaminants like PFAS in hatcheries or other areas where fish congregate in high densities.

CONCLUSIONS AND FUTURE RESEARCH

1. CONCLUSIONS

The purpose of this research was to investigate the effects of PFAS contamination on the population abundance of valuable fisheries in Lake Michigan, along with the impact that PFAS has on the spread of infectious pathogens throughout these fish populations. In chapter one, I created an age structured, discrete, population model to simulate the population abundance of lake whitefish, lake trout and steelhead trout. I ran simulations with different population exposure levels to four different PFAS effects, which were, decreased weight at age, increased disease mortality, reduced fecundity and reduced egg survival. The output of the model gave total population abundance and total egg abundance. In chapter two, I used a SIR model to simulate the dynamics of lake whitefish exposed to VHSV, lake trout exposed to EEDV, and steelhead trout exposed to *F. psychrophilum*. I used data from a preliminary study about lake trout exposed to EEDV and PFOS to decrease the recovery rates and increase the transmission coefficients and mortality rates to simulate the potential impacts of PFAS exposure.

The Leslie matrix model in chapter one provided valuable insight on how the potential effects observed from PFAS exposure could impact fish at the population level. Across all three species, the individual effect that resulted in the largest percent change in population and egg abundance was the decreased weight at age, followed by the reduced number of eggs per kg of fish. These population level responses are the result of individual changes in fish exposed to PFAS. Jantzen et al. found that exposure to PFOA resulted in increased expression of the *c-fos* transcript, which is involved in stress response and ultimately plays a role in the larval growth and protein transport in zebrafish (2016). Fish exposed to high levels of these toxic compounds, and experiencing higher levels of stress, may in turn have less energy to attribute to reproduction which ultimately impacts population levels (Schreck, 2010).

Of all three model species, the steelhead trout models showed the largest percentage change in egg abundance from baseline simulations for reduced fecundity, reduced egg survival, reduced weight, and the combination of all effects. All three species showed similar levels of percent change in population abundance for the simulation with all effects, while steelhead trout showed the largest percent change for both exposures to reduced fecundity and the 50% exposure to reduced weight at age. In terms of population abundance, lake trout showed the largest percentage change for the 50% exposure to reduced weight at age and the 100% exposure to increased disease mortality.

The SIR model presented in chapter 2 found that in the baseline simulations, the infection seemed to decline from day 1 for all three species, with lake trout experiencing the highest percentage of recovered fish compared to lake whitefish and steelhead. When they were exposed to the PFOS effects, steelhead showed the largest percent change in the maximum proportion of infected fish throughout the simulation, followed by lake trout and lake whitefish. When population densities were doubled for each species, all three species showed increased proportions of the population in the infected state and a large majority of the population reached the recovered state by day 365. When PFOS effects were incorporated into this increased density simulation, lake whitefish showed the largest percentage change in the maximum proportion of infected fish. This was likely the result of doubling an already large density of over 7 fish per hectare compared to the other two species whose densities were less than 1.5 fish per hectare.

2. FUTURE RESEARCH

Although there is a large body of literature surrounding PFAS research, there are still a lot of gaps in our knowledge about how these compounds interact with valuable fish and wildlife. There are over 12,000 different types of PFAS chemicals, and other than PFOS and

PFOA, many have not been studied and little is known about their toxicity (Lewis et al., 2022 and USGS, 2023). There are also major gaps in our research on PFAS exposure to sediment dwelling organisms and amphibians, along with PFAS toxicity testing in marine environments (McCarthy et al., 2017). There are many other aspects of PFAS that need further research to assess their impact on human, wildlife and environmental health and until we have this research, the management of this problem will be extremely difficult to navigate.

Research at Michigan State University is beginning disease challenge experiment studies to investigate the effects of PFOS exposure on lake whitefish exposed to VHSV, lake trout exposed to EEDV, and steelhead trout exposed to *F. psychrophilum* (Manliclic, Unpublished). The data from these studies will provide critical information about how exposure to PFOS can impact fishes ability to become infected with threatening pathogens, it will also provide insight on if exposure to PFAS increases mortality resulting from infections. The data from these experiments can be applied to both the Leslie matrix model from chapter 1 and the SIR model from chapter 2. Preliminary data from an EEDV exposure to lake trout showed that the trout exposed to both PFOS and EEDV experience increased mortality throughout a 28-day experiment in comparison to fish that were only exposed to EEDV (Manliclic, Unpublished). On days 16 and 22, single mortalities were seen in the PFOS treatment groups resulting in 25% mortality across the entire experiment. The results from the full length, 56-day study showed that there were 10 mortalities in the PFOS/EEDV treatment group while the EEDV only group only experienced 5 mortalities. These findings highlight the need to continue researching how PFAS interact with wildlife to accurately inform models and make educated management decisions to protect valuable species. The increased disease mortality and immune system effects from PFAS exposure, in combination with other stressors like climate change, invasive species, overharvesting and contamination from other toxic chemicals, can threaten the health of fish populations.

In the future, there is a need to study how PFAS affects a variety of species that are economically and culturally valuable, along with species that play key roles in balancing the ecosystem. To properly manage fisheries, we need a better understanding of which species are bioaccumulating these chemicals, how they can depurate them, how their diet contributes to their exposures, which ages are most sensitive to exposures and how they are impacted by mixtures of PFAS rather than just one compound. Additionally, we need to further our understanding of precursors and their biotransformation into more harmful PFAS compounds (Lewis et al., 2022).

Overall, the models presented in this thesis aim to incorporate the current literature regarding PFAS exposure to Great Lakes fish with their population and disease dynamics to better manage their populations. While there is a need for more research in this area, these models provide insight and a good framework from which to build in some of the main effects of PFAS exposure that could lead to declines in population levels and transmission of harmful pathogens.

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APPENDIX

Table A1.12 Model input parameters for all three species and all management units of lake whitefish and lake trout. PFAS eggs/kg, PFAS disease mortality and PFAS egg survival values were calculated by changing the control values to reflect the PFAS exposure effects listed in section 2.7 of Chapter 1.

Species	Management Unit	Control Eggs/Kg	PFAS Eggs/Kg	Control Disease Mortality	PFAS Disease Mortality	Egg Survival	PFAS Egg Survival
Lake Whitefish	WFM-01	19000	15257	0.02964	0.0247	1.81E-04	1.55E-04
Lake Whitefish	WFM-02	19000	15257	0.02964	0.0247	1.13E-04	9.69E-05
Lake Whitefish	WFM-03	19000	15257	0.02964	0.0247	3.47E-04	2.98E-04
Lake Whitefish	WFM-04	19000	15257	0.02964	0.0247	8.41E-05	7.21E-05
Lake Whitefish	WFM-05	19000	15257	0.02964	0.0247	8.65E-05	7.41E-05
Lake Whitefish	WFM-06	19000	15257	0.02964	0.0247	9.37E-05	8.03E-05
Lake Whitefish	WFM-08	19000	15257	0.02964	0.0247	7.89E-05	6.76E-05
Lake Trout	MM-123	1508	1210.92	0.03612	0.0301	2.95E-03	2.53E-03
Lake Trout	MM-4	1508	1210.92	0.03612	0.0301	2.64E-03	2.26E-03
Lake Trout	MM-5	1508	1210.92	0.03612	0.0301	3.38E-03	2.90E-03
Lake Trout	MM-67	1508	1210.92	0.03612	0.0301	1.55E-03	1.32E-03
Steelhead Trout	Lake Michigan	1139.75	915.217	0.0504	0.042	2.34E-04	2.00E-04

Table A1.13 Lake whitefish WFM-01 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-01	0	0	0.99981877	0	NA	NA
		1	0.12959089	0.3	0	NA	NA
		2	0.12959089	0.3	0	NA	NA
		3	0.000618968	0.170907999	0.018	0.55	0.39875
		4	0.015893973	0.169516766	0.3226	0.538387	0.39033058
		5	0.042076869	0.167114682	0.4892	0.619366	0.44904035
		6	0.08111299	0.163490711	0.6794	0.680318	0.49323055
		7	0.115621135	0.160242072	0.805	0.703271	0.50987148
		8	0.152632889	0.156707766	0.9496	0.737354	0.53458165
		9	0.173342488	0.154706308	0.9552	0.888713	0.64431693
		10	0.17288911	0.154750282	0.9872	0.99496	0.721346
		11	0.157456352	0.156243187	0.9986	1.10947	0.80436575
		12	0.141118797	0.157813012	1	1.17629	0.85281025
		13	0.125551829	0.159298999	1	1.2358	0.895955
		14	0.109039393	0.160865072	1	1.34022	0.9716595
		15	0.098325366	0.161875776	1	1.58113	1.14631925
		16	0.090631966	0.162598898	1	1.44036	1.044261
		17	0.07998313	0.163596351	1	1.40927	1.02172075
		18	0.076467469	0.163924748	1	1.53993	1.11644925
		19	0.06957327	0.16456748	1	1.56681	1.13593725
		20+	0.088557313	0.162793537	1	1.574971667	1.14185446

Table A1.14 Lake whitefish WFM-02 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-02	0	0	0.9998869	0	NA	NA
		1	0.079631718	0.3	0	NA	NA
		2	0.079631718	0.3	0	NA	NA
		3	0.000588136	0.172652729	0.018	0.273142	0.19802795
		4	0.007324205	0.172033493	0.3226	0.450734	0.32678215
		5	0.030725136	0.169870946	0.4892	0.689964	0.5002239
		6	0.058358783	0.16729386	0.6794	0.781347	0.56647658
		7	0.075249157	0.165705738	0.805	1.04104	0.754754
		8	0.086868435	0.164607392	0.9496	1.15436	0.836911
		9	0.096721198	0.163672151	0.9552	1.20239	0.87173275
		10	0.101902381	0.163178928	0.9872	1.32318	0.9593055
		11	0.103902093	0.162988301	0.9986	1.3604	0.98629
		12	0.10521742	0.162862811	1	1.44756	1.049481
		13	0.105968802	0.162791127	1	1.28257	0.92986325
		14	0.107199932	0.162673584	1	1.27633	0.92533925
		15	0.1077069	0.162625172	1	1.29879	0.94162275
		16	0.106306763	0.16275888	1	1.30278	0.9445155
		17	0.106494851	0.162740909	1	1.31072	0.950272
		18	0.10636848	0.162752987	1	1.36119	0.98686275
		19	0.107256606	0.162668188	1	1.2337	0.8944325
		20+	0.108256875	0.162572652	1	1.115	0.808375

Table A1.15 Lake whitefish WFM-03 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-03	0	0	0.9996527	0	NA	NA
		1	0.167957597	0.3	0	NA	NA
		2	0.167957597	0.3	0	NA	NA
		3	0.167957597	0.3	0.018	0.6372001	0.46197007
		4	0.006537	0.182946573	0.3226	0.45151	0.32734475
		5	0.038689096	0.17977093	0.4892	0.690849	0.50086553
		6	0.102005197	0.173407082	0.6794	0.782051	0.56698698
		7	0.156021679	0.167852235	0.805	1.04174	0.7552615
		8	0.200279946	0.1632058	0.9496	1.15495	0.83733875
		9	0.245922098	0.158315862	0.9552	1.2029	0.8721025
		10	0.270552752	0.155632228	0.9872	1.32376	0.959726
		11	0.283392042	0.154220122	0.9986	1.36092	0.986667
		12	0.291898019	0.153279446	1	1.44777	1.04963325
		13	0.295596728	0.152869115	1	1.28272	0.929972
		14	0.30484844	0.151839211	1	1.27465	0.92412125
		15+	0.308956667	0.151380254	1	1.289	0.934525

Table A1.16 Lake whitefish WFM-04 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-04	0	0	0.9999159	0	NA	NA
		1	0.0520834	0.3	0	NA	NA
		2	0.0520834	0.3	0	NA	NA
		3	0.000805902	0.205377248	0.018	0.575446	0.41719835
		4	0.006818117	0.204711472	0.3226	0.811458	0.58830705
		5	0.025531504	0.202630142	0.4892	1.01184	0.733584
		6	0.063635444	0.198348722	0.6794	1.333	0.966425
		7	0.069660738	0.197666218	0.805	1.33074	0.9647865
		8	0.080726691	0.196408617	0.9496	1.73313	1.25651925
		9	0.080683696	0.196413504	0.9552	1.906	1.38185
		10	0.080061384	0.196484371	0.9872	1.94444	1.409719
		11	0.079775266	0.196516982	0.9986	2.022	1.46595
		12	0.080882282	0.196390911	1	1.861	1.349225
		13	0.080626785	0.196419989	1	1.80882	1.3113945
		14	0.077358914	0.196791903	1	2.01	1.45725
		15	0.078282969	0.196686794	1	1.765	1.279625
		16+	0.074379678	0.197130568	1	2.161	1.566725

Table A1.17 Lake whitefish WFM-05 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-05	0	0	0.9999135	0	NA	NA
		1	0.052582335	0.3	0	NA	NA
		2	0.052582335	0.3	0	NA	NA
		3	0.00128475	0.179012627	0.018	0.279182	0.20240695
		4	0.012349779	0.177953962	0.3226	0.513	0.371925
		5	0.031525732	0.176109487	0.4892	0.616	0.4466
		6	0.055872399	0.173749387	0.6794	0.791	0.573475
		7	0.06624592	0.172737373	0.805	0.897	0.650325
		8	0.071346212	0.172238379	0.9496	1.05785	0.76694125
		9	0.076384762	0.171744491	0.9552	1.529	1.108525
		10	0.076179622	0.171764615	0.9872	1.66034	1.2037465
		11	0.07332069	0.17204496	0.9986	2.0922	1.516845
		12	0.064520541	0.172905964	1	2.61565	1.89634625
		13	0.064210107	0.172936281	1	2.31923	1.68144175
		14	0.057156213	0.173624347	1	2.66241	1.93024725
		15	0.059420938	0.173403638	1	2.58399	1.87339275
		16	0.0569635	0.173643128	1	2.70028	1.957703
		17	0.059534227	0.173392567	1	2.5613	1.8569425
		18	0.055657117	0.173770347	1	2.51842	1.8258545
		19	0.058866819	0.173599145	1	2.4945	1.8085125
		20+	0.055284558	0.173555194	1	2.765	2.004625

Table A1.18 Lake whitefish WFM-06 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-06	0	0	0.9999063	0	NA	NA
		1	0.052834249	0.3	0	NA	NA
		2	0.052834249	0.3	0	NA	NA
		3	0.00048009	0.18026383	0.018	0.474067	0.34369858
		4	0.012052243	0.179149086	0.3226	0.670634	0.48620965
		5	0.035555244	0.176871087	0.4892	0.806927	0.58502208
		6	0.057991127	0.174678494	0.6794	0.859578	0.62319405
		7	0.074869919	0.173017012	0.805	1.0008	0.72558
		8	0.086569039	0.171859211	0.9496	1.27372	0.923447
		9	0.092867343	0.171233718	0.9552	1.16313	0.84326925
		10	0.096039151	0.170918177	0.9872	1.2661	0.9179225
		11	0.097685518	0.170754237	0.9986	1.41646	1.0269335
		12	0.098548913	0.170668199	1	1.49678	1.0851655
		13	0.099194749	0.170603834	1	1.50639	1.09213275
		14	0.099625403	0.170560884	1	1.60653	1.16473425
		15	0.099875806	0.170535932	1	1.67329	1.21313525
		16	0.100023112	0.170521228	1	1.72314	1.2492765
		17	0.10009482	0.170514087	1	1.86365	1.35114625
		18	0.100158882	0.170507722	1	1.73613	1.25869425
		19	0.100111783	0.170512423	1	1.92681	1.39693725
		20+	0.100026833	0.170520905	1	1.94	1.4065

Table A1.19 Lake whitefish WFM-08 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Whitefish	WFM-08	0	0	0.9999211	0	NA	NA
		1	0.061935781	0.3	0	NA	NA
		2	0.061935781	0.3	0	NA	NA
		3	0.000896297	0.179214608	0.018	0.691442	0.50129545
		4	0.014547663	0.177906772	0.35	0.916236	0.6642711
		5	0.04687686	0.174784353	0.496	1.08471	0.78641475
		6	0.062211956	0.173290457	0.681	1.21243	0.87901175
		7	0.067320949	0.17279087	0.807	1.30613	0.94694425
		8	0.068831241	0.172642997	0.951	1.37646	0.9979335
		9	0.069561175	0.172571521	0.955	1.41993	1.02944925
		10	0.069919571	0.172536415	0.984	1.44993	1.05119925
		11	0.070156537	0.172513198	1	1.47333	1.06816425
		12	0.070310684	0.172498078	1	1.48342	1.0754795
		13	0.070383723	0.172490905	1	1.45573	1.05540425
		14	0.070428726	0.17248653	1	1.70365	1.23514625
		15	0.070379047	0.172491383	1	1.56337	1.13344325
		16	0.07036667	0.172492583	1	1.55	1.12375
		17	0.07035985	0.172493241	1	1.55351	1.12629475
		18	0.070367435	0.172492534	1	1.48	1.073
		19	0.070391036	0.172490215	1	1.47	1.06575
		20+	0.070548419	0.172474783	1	1.538873333	1.11568317

Table A1.20 Lake trout MM-123 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Trout	MM-123	0	0	0.997053	0	NA	NA
		1	0.000201439	0.625915096	0.000236842	0.036	0.0261
		2	0.032823657	0.20690817	0.001236842	0.395	0.286375
		3	0.101399375	0.198925124	0.037368421	0.902	0.65395
		4	0.222769687	0.18424225	0.151342105	1.549	1.123025
		5	0.347189985	0.168287614	0.470973684	2.204	1.5979
		6	0.422455424	0.1580736	0.823868421	2.773	2.010425
		7	0.444896157	0.154929488	0.958052632	3.253	2.358425
		8	0.430413569	0.156964208	0.990710526	3.646	2.64335
		9	0.394089446	0.161980216	0.997710526	3.931	2.849975
		10	0.348622473	0.168097607	0.999684211	4.194	3.04065
		11	0.302779869	0.174102911	0.999973684	4.39	3.18275
		12	0.261473413	0.179388289	1	4.456	3.2306
		13	0.227481313	0.183656168	1	4.552	3.3002
		14	0.201020123	0.186931071	1	4.642	3.36545
		15+	0.180960486	0.18938751	1	4.694	3.40315

Table A1.21 Lake trout MM-4 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Trout	MM-4	0	0	0.997361	0	NA	NA
		1	9.30E-08	0.586299436	0	0.036	0.0261
		2	0.000364799	0.217921389	0	0.321	0.232725
		3	0.032566119	0.214103023	0.02	0.713	0.516925
		4	0.108327818	0.204939471	0.08	1.215	0.880875
		5	0.230295165	0.18957974	0.292	1.711	1.240475
		6	0.338490999	0.175187893	0.67	2.277	1.650825
		7	0.387674887	0.168353715	0.902	2.762	2.00245
		8	0.393706732	0.167501257	0.974	2.97	2.15325
		9	0.37429482	0.170233182	0.993	3.328	2.4128
		10	0.340399535	0.174926424	0.998	3.649	2.645525
		11	0.300311771	0.180360312	1	3.929	2.848525
		12	0.260001945	0.185707749	1	4.152	3.0102
		13	0.223645909	0.190438825	1	4.299	3.116775
		14	0.192876548	0.194379833	1	4.441	3.219725
		15+	0.167496376	0.197589681	1	4.56	3.306

Table A1.22 Lake trout MM-5 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Trout	MM-5	0	0	0.9966155	0	NA	NA
		1	2.00E-06	0.784826849	0	0.036	0.0261
		2	0.008055574	0.185333745	0	0.402	0.29145
		3	0.045939378	0.181529961	0.063	0.866	0.62785
		4	0.134176459	0.172459557	0.157	1.441	1.044725
		5	0.241296193	0.160992654	0.351	2.064	1.4964
		6	0.326319526	0.151464132	0.611	2.695	1.953875
		7	0.370052985	0.146388421	0.804	3.274	2.37365
		8	0.375286957	0.145772122	0.906	3.858	2.79705
		9	0.349697091	0.148766967	0.956	4.21	3.05225
		10	0.305583328	0.153827296	0.979	4.57	3.31325
		11	0.255255096	0.159456429	0.991	4.916	3.5641
		12	0.207397864	0.164681034	0.996	5.126	3.71635
		13	0.168932275	0.168797978	0.998	5.272	3.8222
		14	0.140715344	0.17177473	0.999	5.402	3.91645
		15+	0.121315089	0.173801225	0.999	5.496	3.9846

Table A1.23 Lake trout MM-67 parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Lake Trout	MM-67	0	0	0.998455	0	NA	NA
		1	0	0.672706071	0	0.036	0.0261
		2	0.00430801	0.197039964	0.002	0.402	0.29145
		3	0.023890779	0.194954428	0.061	0.866	0.62785
		4	0.067681424	0.190237807	0.149	1.441	1.044725
		5	0.133952403	0.182949644	0.34	2.064	1.4964
		6	0.20389529	0.175037905	0.602	2.695	1.953875
		7	0.255834224	0.168999307	0.8	3.274	2.37365
		8	0.280101895	0.166125026	0.904	3.858	2.79705
		9	0.277759302	0.166404461	0.955	4.21	3.05225
		10	0.255371719	0.169054188	0.979	4.57	3.31325
		11	0.221928334	0.172957715	0.99	4.916	3.5641
		12	0.185823724	0.177105312	0.996	5.126	3.71635
		13	0.153155024	0.180801166	0.998	5.272	3.8222
		14	0.126699718	0.183755937	0.999	5.402	3.91645
		15+	0.107244713	0.18590999	0.999	5.496	3.9846

Table A1.24 Steelhead trout parameter values used for the model input. These parameters include discrete fishing mortality and discrete natural mortality which make up the survival probability in the Leslie matrix. The other parameters listed are the proportion of mature fish, weight of baseline fish and weight of PFAS contaminated fish. These parameters are used for assessing fecundity in row 0 of the Leslie matrix.

Species	Management Unit	Age	Discrete Fishing Mortality	Discrete Natural Mortality	Proportion of Mature Fish	Control Weight (Kg)	PFAS Weight (Kg)
Steelhead Trout	Lake Michigan	0	0	0.9997661	0	NA	NA
		1	0.00028822	0.255054581	0.209772727	0.840590909	0.60942841
		2	0.006514727	0.146935965	0.419636364	1.836227273	1.33126477
		3	0.042599623	0.205226108	0.669272727	2.838318182	2.05778068
		4	0.064829674	0.238553802	0.769522727	3.649181818	2.64565682
		5	0.069716153	0.248991768	0.8135	4.216863636	3.05722614
		6	0.070813964	0.266383125	0.929318182	4.635045455	3.36040796
		7+	0.071203488	0.276713301	1	4.953772727	3.59148523

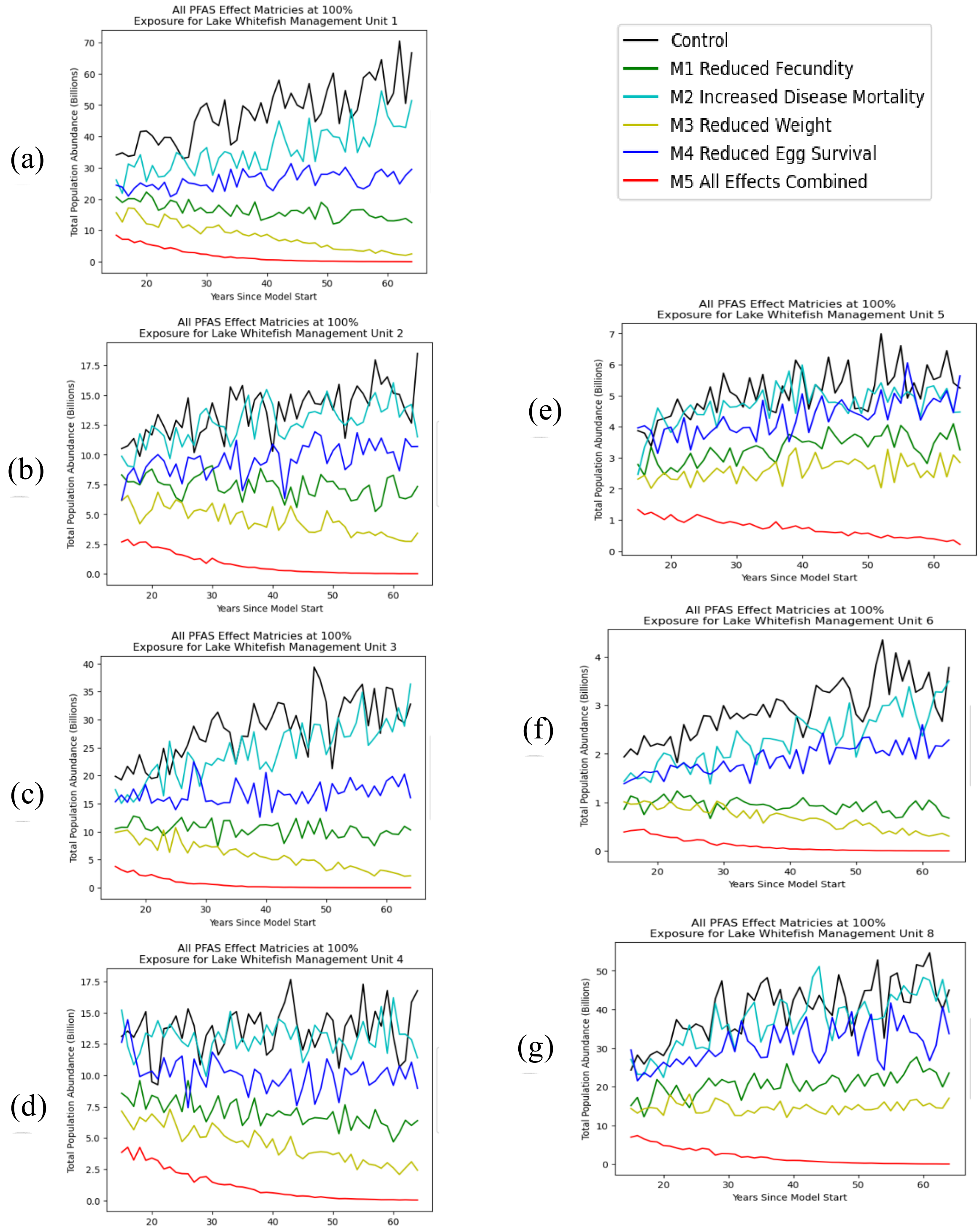

Figure A1.16 Total population abundance for each individual lake whitefish management units simulated over 65 years. The first 15 years were not shown to eliminate initial fluctuations in abundance. Individual PFAS effects are shown using the lines labeled M1-M4 with 100% of the population being exposed to each effect. A combination of all PFAS effects is shown with the red line labeled M5. The black line represents population abundance under baseline conditions with no PFAS effects included.

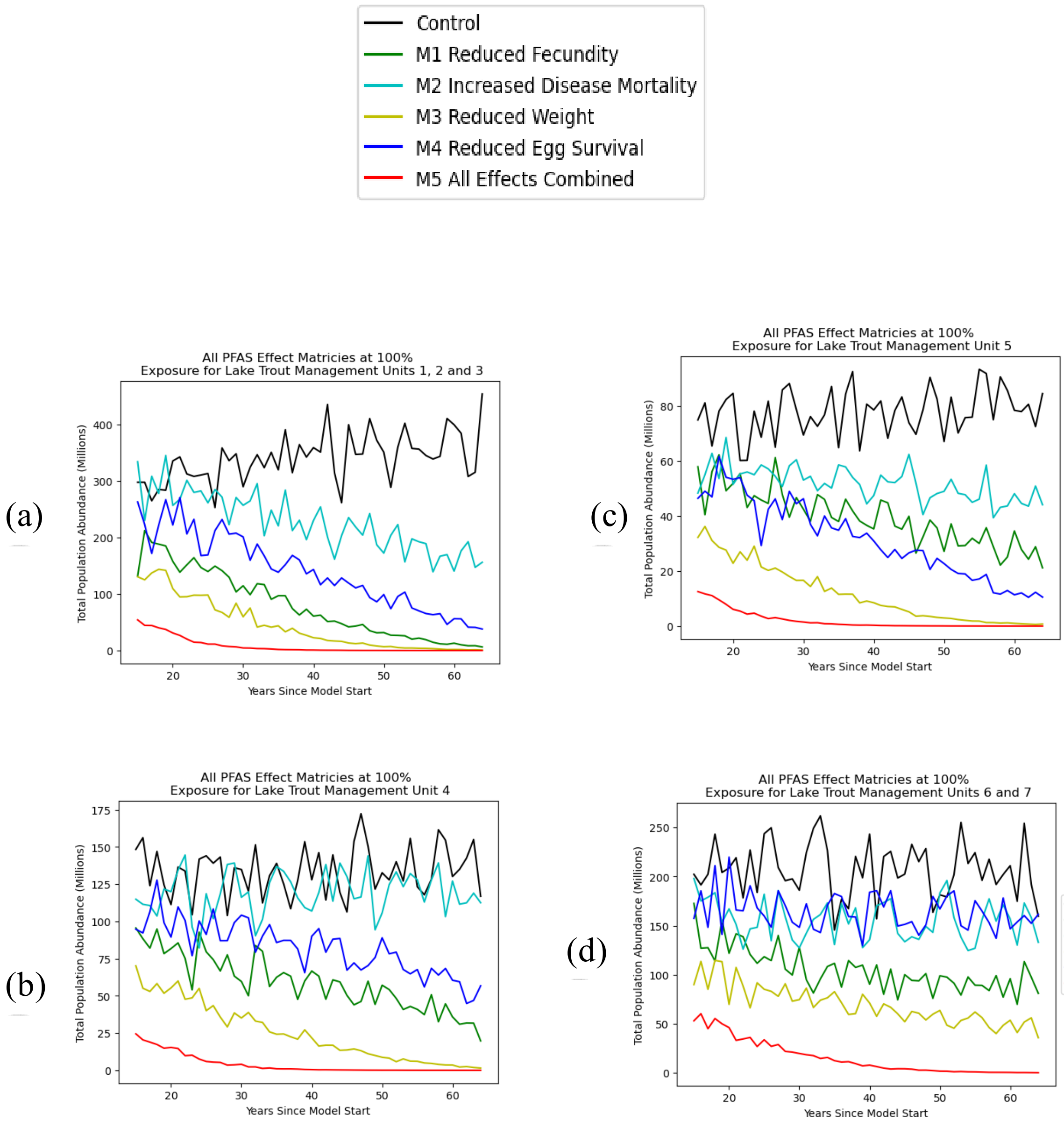

Figure A1.17 Total population abundance for each individual lake trout management units simulated over 65 years. The first 15 years were not shown to eliminate initial fluctuations in abundance. Individual PFAS effects are shown using the lines labeled M1-M4 with 100% of the population being exposed to each effect. A combination of all PFAS effects is shown with the red line labeled M5. The black line represents population abundance under baseline.

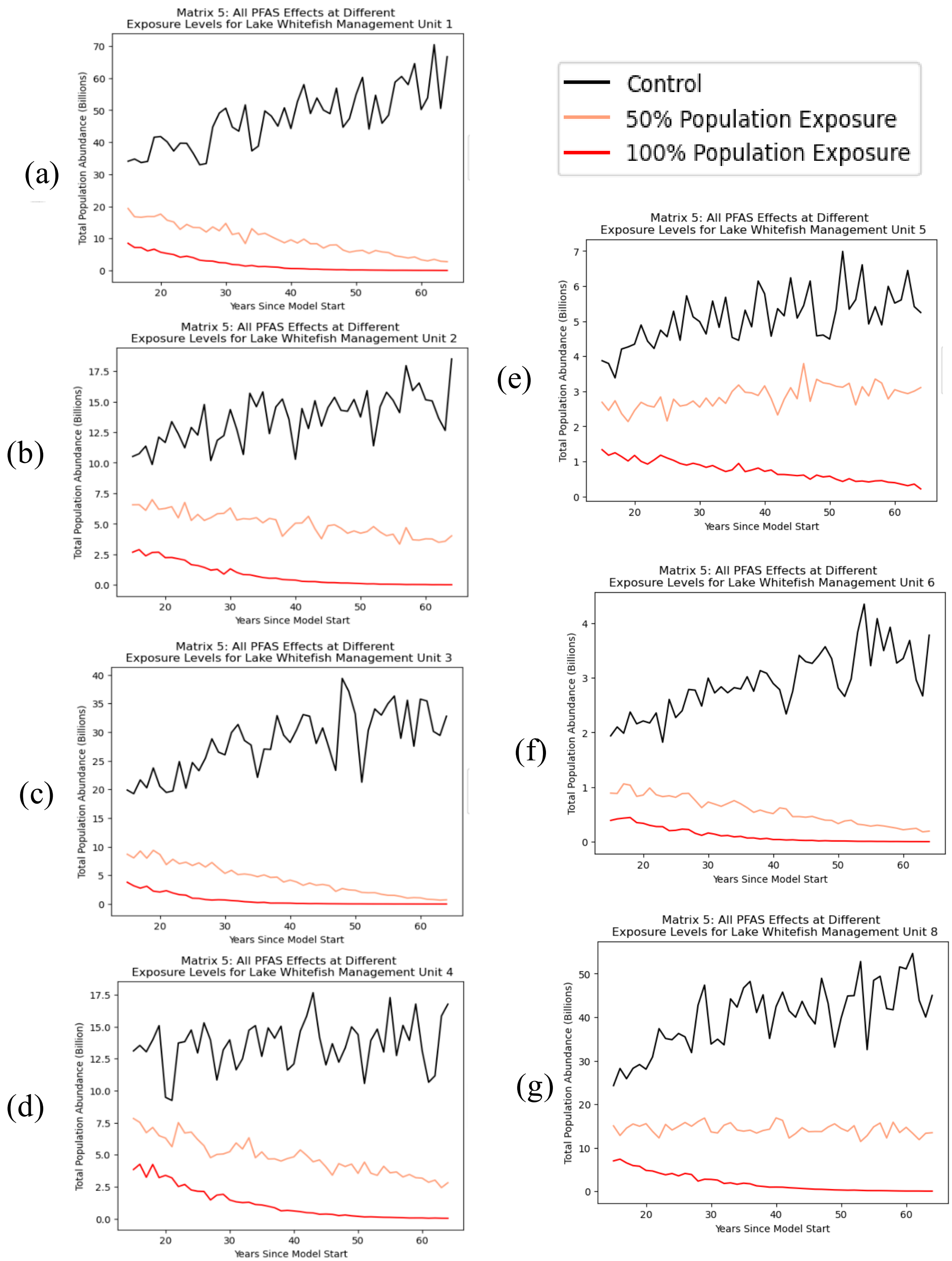

Figure A1.18 Total population abundance of fish ages 0-20+ for each individual lake whitefish management unit simulated over 65 years. The first 15 years were not shown to eliminate initial fluctuations in abundance. This simulation shows the population model using the Leslie matrix including all possible PFAS effects: reduced fecundity, weight and egg survival along with increased disease mortality. This matrix was used with 0%, 50% and 100% of the population being exposed to these PFAS effects.

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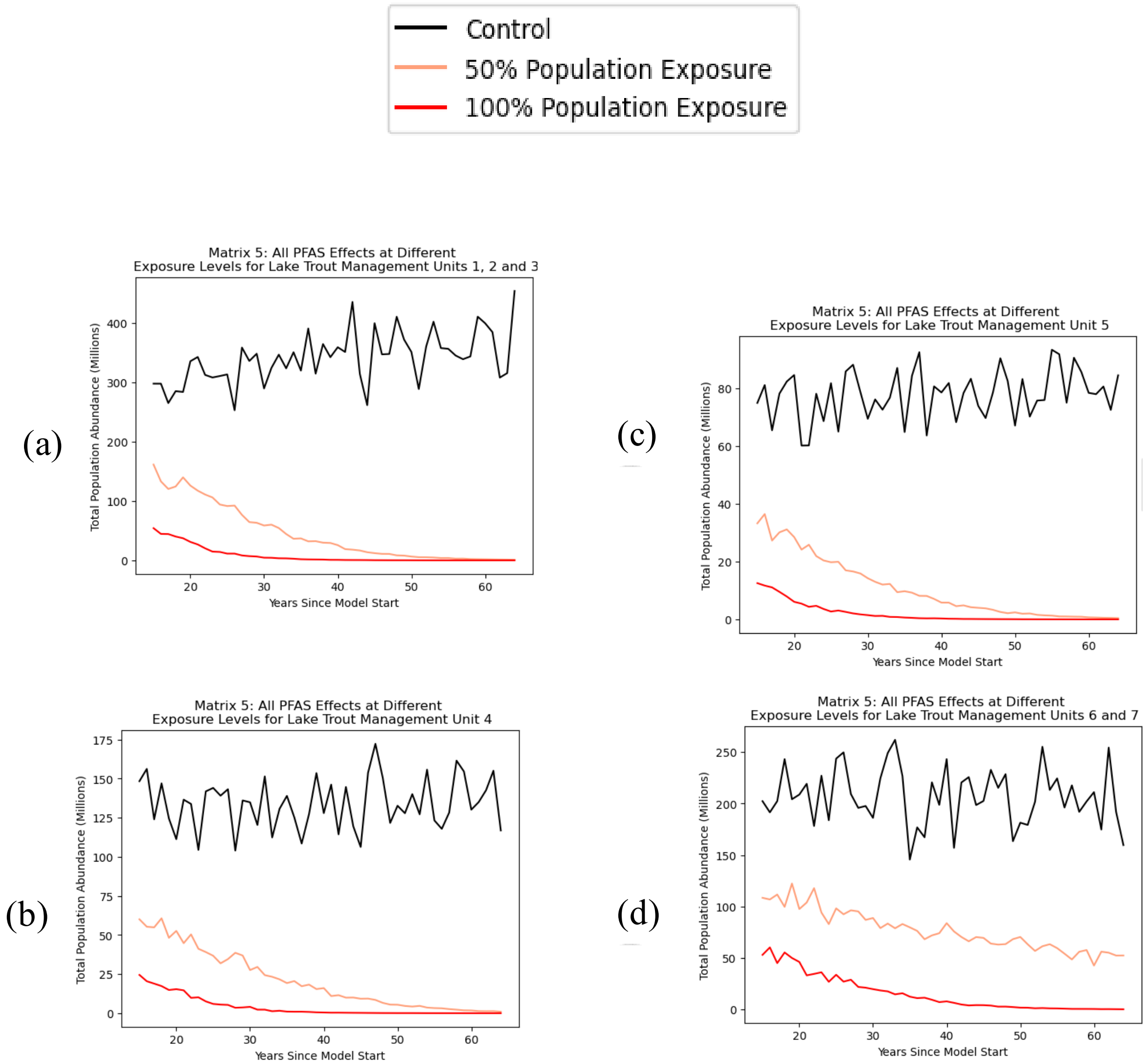

Figure A1.19 Total population abundance of fish ages 0-20+ for each individual lake trout management unit simulated over 65 years. The first 15 years were not shown to eliminate initial fluctuations in abundance. This simulation shows the population model using the Leslie matrix including all possible PFAS effects: reduced fecundity, weight and egg survival along with increased disease mortality. This matrix was used with 0%, 50% and 100% of the population being exposed to these PFAS effects.

(a)

(b)

(c)

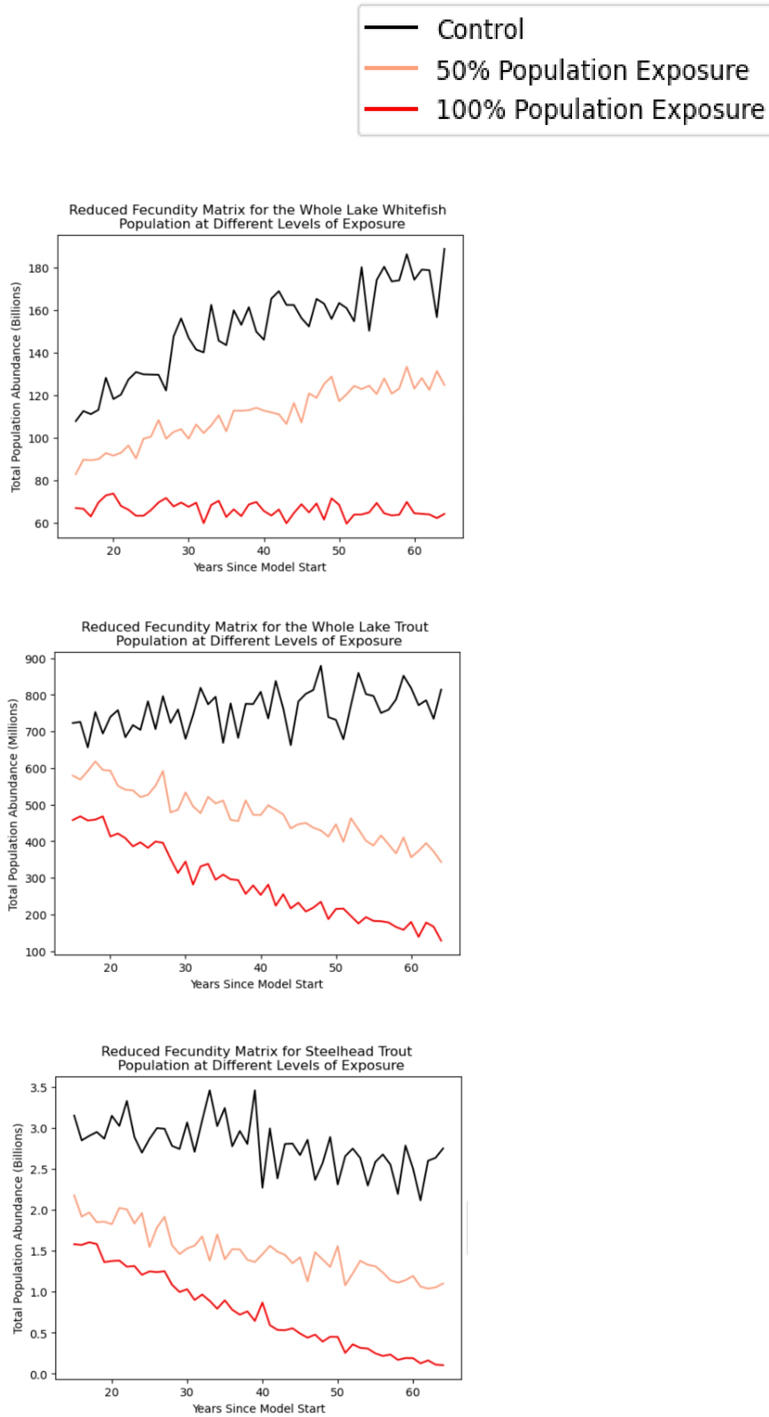

Figure A1.20 Total population abundance of fish using the reduced fecundity matrix for all three species. The last 50 years of a 65-year simulation are shown to eliminate the initial fluctuations in abundance within the first 15 years. Simulations were done with either 0%, 50% or 100% of the population being exposed to the reduced fecundity effect. (a) shows the lake whitefish, (b) shows the lake trout and (c) shows the steelhead trout models with the abundance calculations including ages 0+.

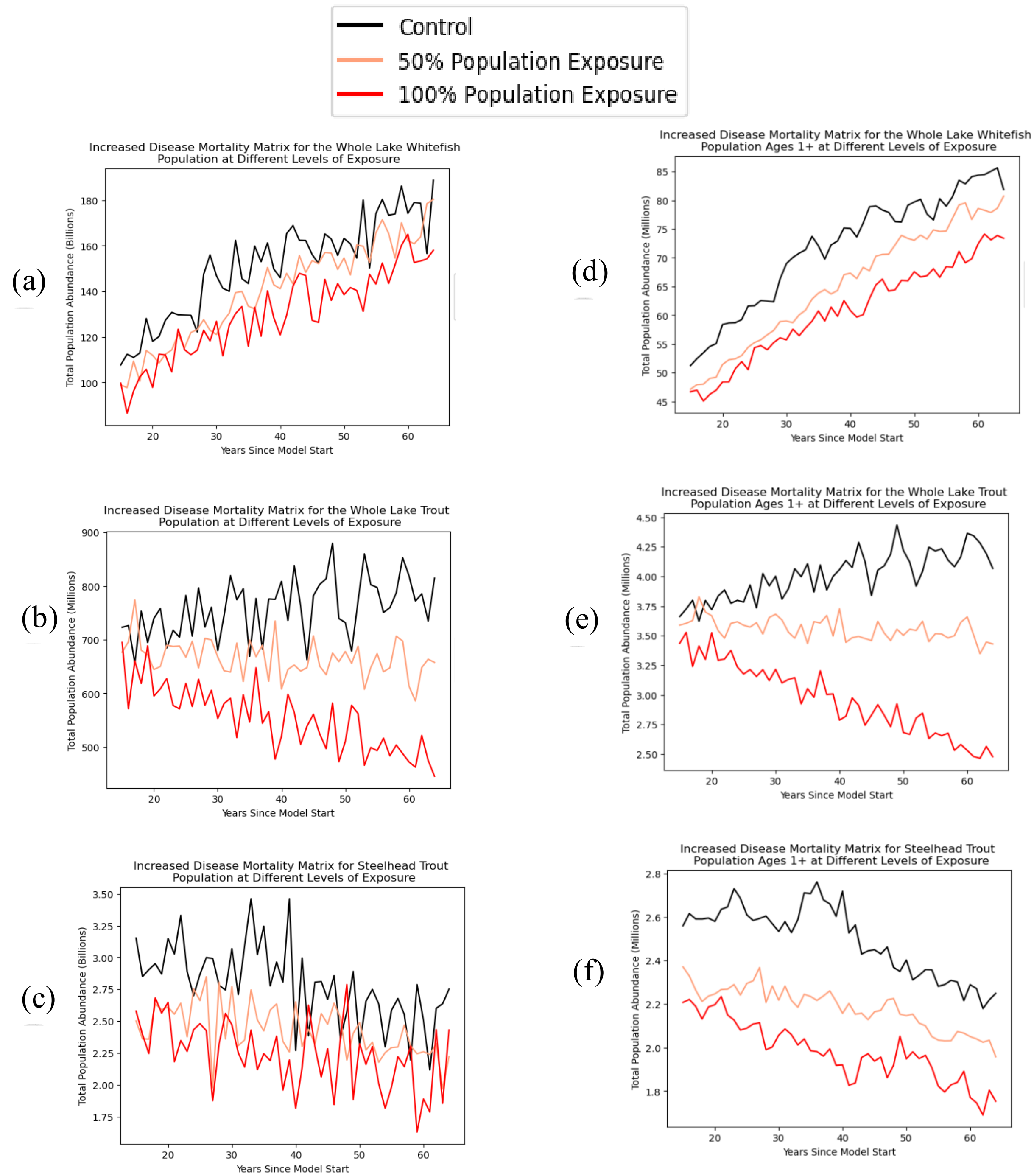

Figure A1.21 Total population abundance of fish using the increased disease mortality matrix for all three species. The last 50 years of a 65-year simulation are shown to eliminate the initial fluctuations in abundance within the first 15 years. Simulations were done with either 0%, 50% or 100% of the population being exposed to the increased disease mortality effect. (a), (b) and (c) show the lake whitefish, lake trout and steelhead trout models with the abundance calculations including age 0 fish while (d), (e) and (f) do not include age 0 in the population count. (a) and (d) are representative of lake whitefish, (b) and (e) show lake trout and (c) and (f) show steelhead trout abundances.

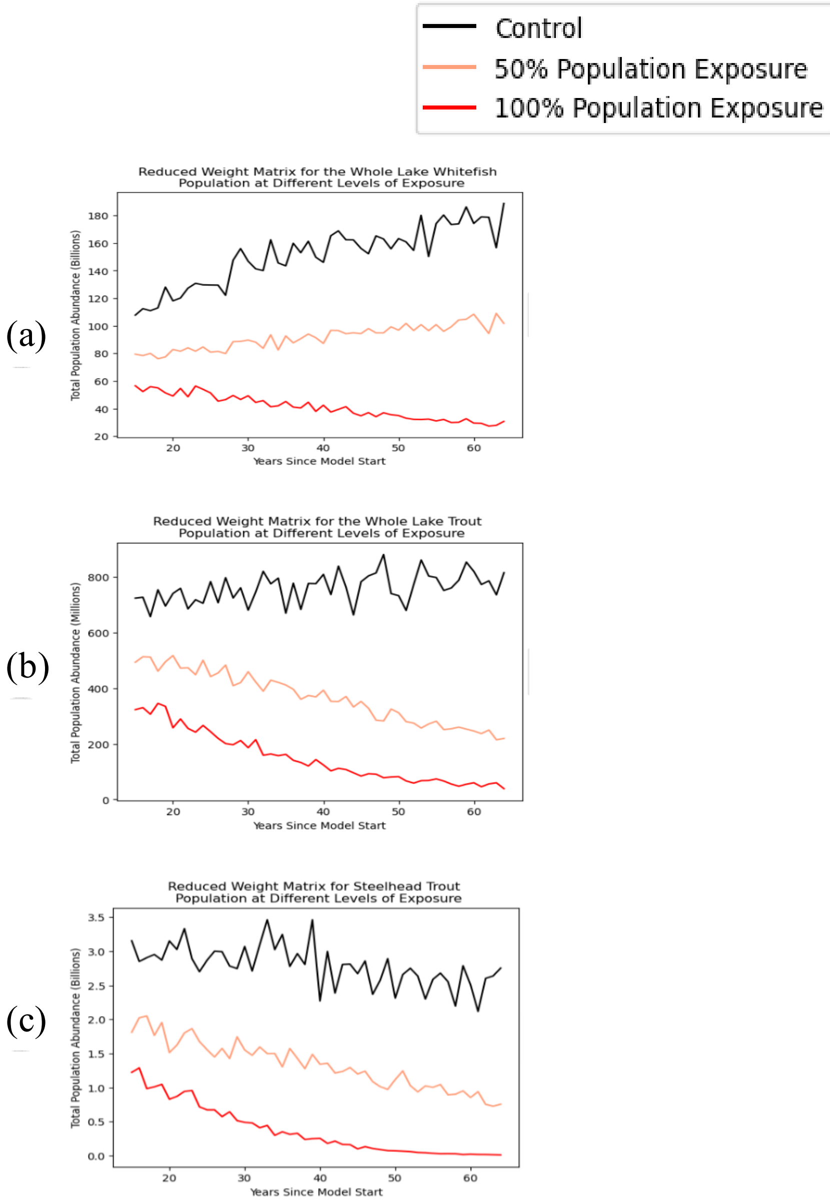

Figure A1.22 Total population abundance of fish using the reduced weight matrix for all three species. The last 50 years of a 65-year simulation are shown to eliminate the initial fluctuations in abundance within the first 15 years. Simulations were done with either 0%, 50% or 100% of the population being exposed to the reduced weight effect. (a) shows the lake whitefish, (b) shows the lake trout and (c) shows the steelhead trout models with the abundance calculations including ages 0+.

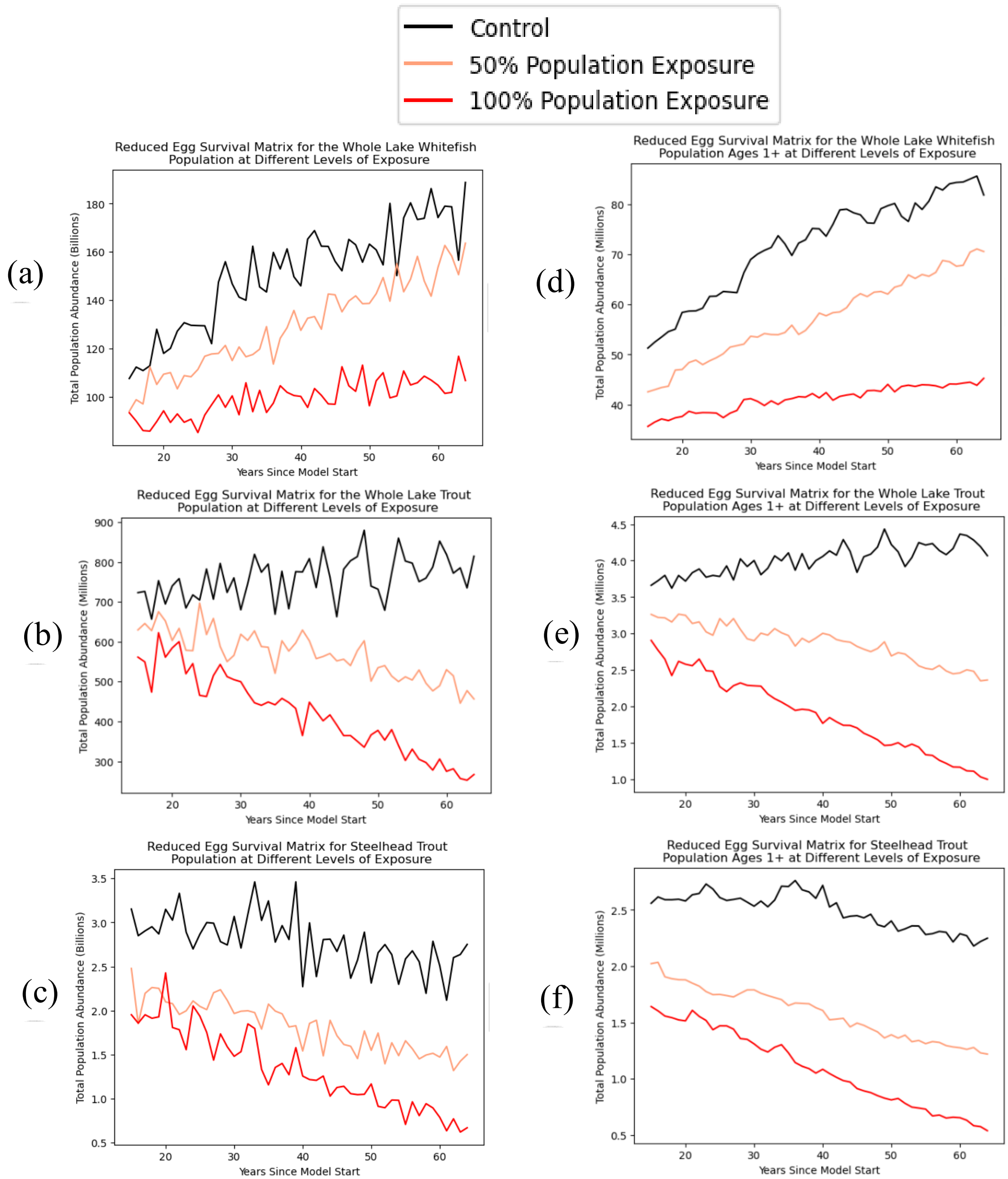

Figure A1.23 Total population abundance of fish using the reduced egg survival matrix for all three species. The last 50 years of a 65-year simulation are shown to eliminate the initial fluctuations in abundance within the first 15 years. Simulations were done with either 0%, 50% or 100% of the population being exposed to the reduced egg survival effect. (a), (b) and (c) show the lake whitefish, lake trout and steelhead trout models with the abundance calculations including age 0 fish while (d), (e) and (f) do not include age 0 in the population count. (a) and (d) are representative of lake whitefish, (b) and (e) show lake trout and (c) and (f) show steelhead trout abundances.

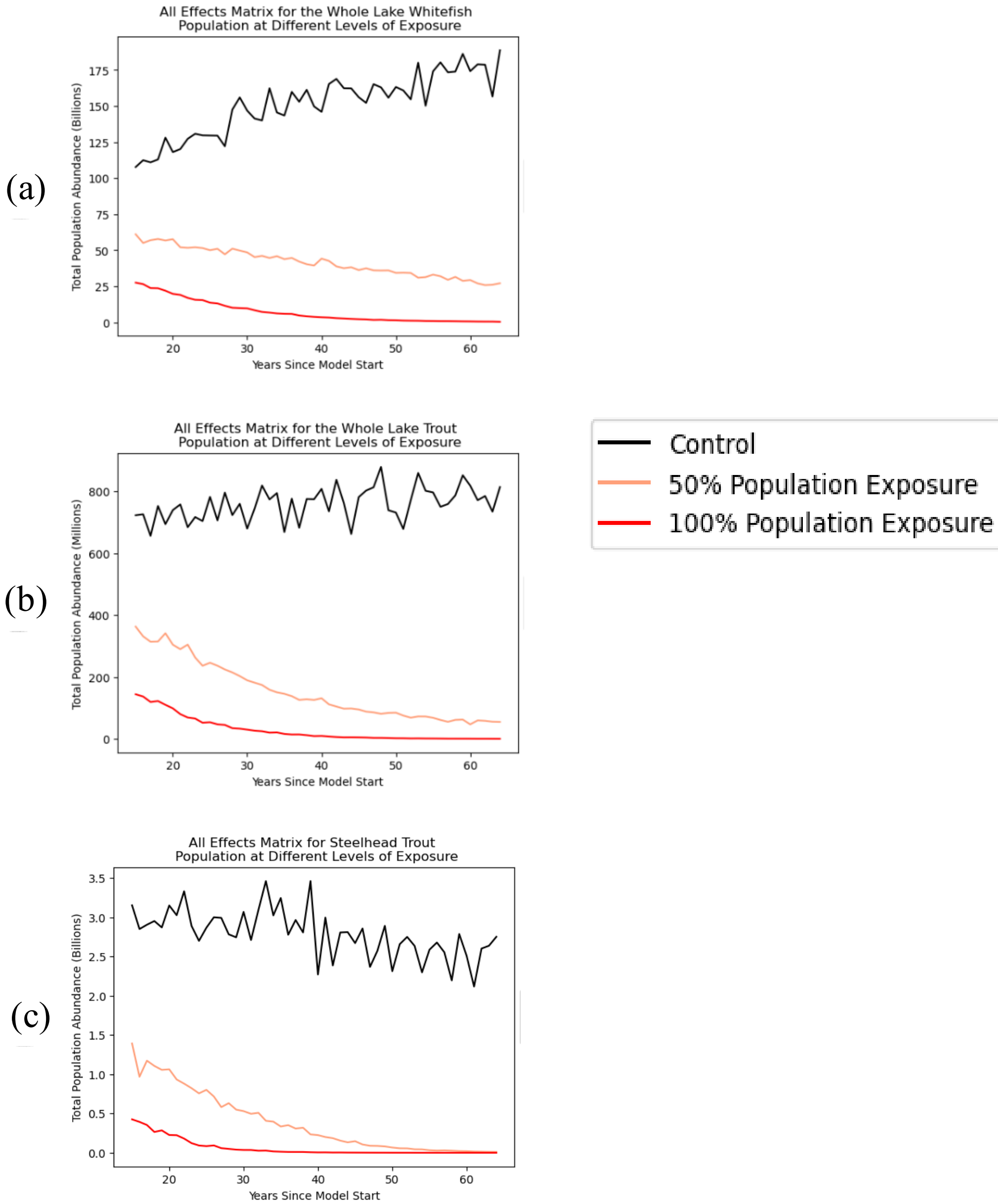

Figure A1.24 Total population abundance of fish using the matrix with al PFAS effects for all three species. The last 50 years of a 65-year simulation are shown to eliminate the initial fluctuations in abundance within the first 15 years. Simulations were done with either 0%, 50% or 100% of the population being exposed to all PFAS effects. (a) shows the lake whitefish, (b) shows the lake trout and (c) shows the steelhead trout models with the abundance calculations including ages 0+.