A DYNAMICAL SYSTEMS APPROACH TO MODELING MERCURY CONTAMINATION IN AQUATIC FOOD WEBS

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A Dynamical Systems Approach to Modeling Mercury Contamination in Aquatic Food Webs

by

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Abstract

Unacceptable mercury levels have frequently been observed in the fish of Boreal forest lake systems. Because of this, fish consumers are at risk for mercury exposure through fish consumption. Populations relying heavily on dietary fish are particularly at risk. The Innu population in Labrador is one such group of people. They catch fish year-round from a variety of lakes in Labrador. Some species of fish harvested by the Innu have been shown to accumulate high levels of mercury that surpass consumption guidelines. This is of great concern because mercury is a neurotoxicant and can have adverse health effects including reproductive impairment, growth inhibition, developmental abnormalities, and altered behavioural responses.

We have developed a dynamical systems model to predict the effect that certain environmental changes have on the mercury content of food fish in lake systems. We model the aquatic system using a system of ordinary differential equations which relate the biomass of fish in the highest trophic levels with the amount of methyl mercury in these fish populations and in the environment. We look at factors such as harvesting rates, intrinsic growth rates of populations, mercury absorption rate, and rate that mercury is introduced to the lake environment. We also examine the effect that seasonal temperatures and spring snow melt has on the system.

Dynamical systems models are often used in biology but have rarely been used to examine situations involving contamination of aquatic environments. The models described here are original models; to our knowledge, these are the first dynamical systems models developed to model an aquatic contaminant that is not lethal to the

population.

The model predicts that when mercury enters the lake at a constant rate a stable equilibrium state will be reached eventually. The time taken to reach this equilibrium will vary depending on rate of mercury input. Using parameter values applicable to Boreal forest lakes, the time taken to reach equilibrium is predicted to be approximately 15-20 years, and the final mercury concentration is predicted to be 0.4 ppm for prey fish and 0.655 ppm for top predator fish. When the seasonal effect of colder temperatures and spring snow melt is considered, the lake system exhibits yearly cyclical behaviour. This model predicts fish mercury concentrations very similar to the nonseasonal model. The models described here were shown to be sensitive to methyl mercury input to the lake, methyl mercury output from the lake, and predator functional response.

Chapter 1

Introduction

Mathematical models can be used to make predictions about specific behaviours and future activity of contaminated systems. Two mathematical models have been developed here to predict the effect that certain environmental changes have on the mercury content of food fish. To date, the majority of mercury models have been statistical models or mass-balance models that do not use dynamical systems analysis but, rather, rely on assigning various values to parameters and running simulations using modeling software (Harris & Bodaly, 1998; Hudson, Gherini, Watras & Porcella, 1994; MacRury, Graeb, Johnson & Clements, 2002).

These are the first dynamical systems models developed to study mercury behaviour in aquatic systems. Other dynamical systems models for contamination of aquatic systems have typically dealt with toxicants that cause very different system behaviour than mercury. These models focus on population depletion factors caused by the introduction of a strong toxicant, including increased death rate due to toxi-

cant, altered feeding behaviour and biomass conversion due to toxicant, and decreased reproduction rate due to toxicant (Thieme, 2003; Freedman & Shukla, 1991). Freedman and Shukla (1991) developed a single-species and predator-prey model in which the pollutant decreased population growth rates, carrying capacity, predator functional response, and food conversion efficiency. Further, the toxicant in this model was absorbed by and removed from the populations at rates directly proportional to the concentration of toxicant in the population.

Similarly, Thieme (2003) modeled an aquatic population interacting with a polluted environment where the pollutant negatively affected food intake and biomass conversion, and increased population mortality. Further, this model considered toxicant intake only through the environment, ignoring the food pathway.

The models outlined and analysed in this study use a system of ordinary differential equations to relate biomass of fish in the highest trophic levels with the amount of mercury in these fish populations and in the environment. These models will provide information and make predictions as to mercury movement between the environment and fish, mercury movement between different trophic levels of fish, and length of time mercury will stay in the system.

1.1 Mercury

Mercury is a naturally occurring, heavy metal that is found in the earth's crust. It is the only metal that is liquid at room temperature. Several forms of mercury exist in the environment including raw, elemental mercury, inorganic mercury, and

organic methyl mercury (National Research Council, 2000). Mercury and its unique properties have been known for thousands of years. In many cultures, mercury was thought to have magical properties and even to prolong life. The ancient Greeks used mercury in ointments and the Romans used it in cosmetics. By 500 BC, mercury was being used to make amalgams with other metals. In more recent times, mercury has been used in a variety of different products including thermometers, barometers, neon signs, energy efficient compact fluorescent light bulbs, automobile sensors, herbicides, and some medications including laxatives and antidepressants. The practice of using mercury in medications and herbicides was largely discontinued when toxic effects of mercury were discovered. There are still some cultures, however, in which mercury is used for folk medicine and ceremonial purposes, and it is still used in dental amalgams in many places.

In the 19th century it was discovered that exposure to high levels of mercury can cause serious health effects in humans. Since then, research has shown many harmful effects of mercury exposure including reproductive impairment, growth inhibition, developmental abnormalities, personality changes, and altered behavioural responses (Beckvar, Field, Salazar & Hoff, 1996). Pregnant women need to monitor mercury consumption because mercury can be transferred to the fetus and can interfere with brain development of the embryo (Clarkson, 1994). In extreme cases, when people are exposed to very high levels of mercury, serious neurological damage can result including numbness in limbs and lips, slurred speech, constricted vision, severe personality changes, and even death.

There is increasing evidence that even low levels of mercury can have significant

effects on human health. Recent studies have demonstrated reproductive and cardiovascular problems in humans that have been exposed to mercury (National Research Council, 2000). The best-known case of human mercury exposure occurred in Minamata, Japan in the 1950s when a chemical plant began dumping mercury-containing waste into Minamata Bay. Local people that were catching and eating fish from the bay began to exhibit very strange symptoms and behaviour including sensory impairment, constriction of visual fields, hearing loss, and speech disturbances (Eisler, 1987). Eventually it was determined that mercury in fish was the cause of the problem but, by that time, thousands of people had been affected. A similar mercury poisoning event occurred in Canada in the 1960s, in the English-Wabigoon River system in northwestern Ontario. In this case, a chemical plant was discharging approximately 3000 lbs of mercury annually between 1962-1970 (Fimreite & Reynolds, 1973). As a result, many First Nations people who ate fish from the English-Wabigoon system experienced health problems associated with mercury poisoning. In addition to the human health issues, there was a serious economic effect whereby commercial fishers lost their source of livelihood as mercury levels in the fish they caught exceeded commercially acceptable limits.

1.2 Mercury in lake systems

Lakes obtain mercury from atmospheric deposition and from soil leaching, with the majority coming from atmospheric deposition (Watras *et al.*, 1995; Fitzgerald, Mason, Vandal & Dulac, 1994). Mercury enters the atmosphere through both natural and

anthropogenic means. Mercury is released naturally from the earth's crust through volcanic activity, weathering of rocks and from the oceans. A significant portion of the atmospheric mercury burden is a result of anthropogenic activities including mining, coal combustion, incineration of mercury-containing items and metal smelting.

The mercury cycle is complex (see Figure 1.1). The forms of mercury most abundant in the atmosphere are elemental mercury (Hg^0) and inorganic mercury (Hg[II]). Elemental mercury has a high vapour pressure, has low solubility, does not combine with inorganic or organic ligands, and is not available for methylation. Inorganic mercury is primarily bound to particulates and organic substances, and makes up most of the mercury that is released into the environment. When inorganic mercury is deposited in aquatic systems, it can be transformed into methyl mercury (Houck & Cech, 2004). Methyl mercury (CH_3Hg^+) is the most toxic form of mercury (National Research Council, 2000). It is extremely mobile, very stable, and can easily penetrate membranes in living organisms (Houck & Cech, 2004).

Mercury has been observed worldwide in a variety of lake environments including many that have no local sources of mercury. Mercury can be transported long distances in the atmosphere due to a long atmospheric residence time of approximately one year (Fitzgerald, 1989). Mercury occurs in the atmosphere almost entirely in its elemental form (Fitzgerald *et al.*, 1994; Porcella, 1994) which can be oxidized to mercuric ion Hg[II] by photocatalytic reactions (Brosset, 1987). Although inorganic Hg[II] and methyl mercury constitute $< 2\%$ of the total mercury concentration in air, the majority of atmospheric mercury deposition is in one of these forms with the vast majority being deposited as inorganic Hg[II] (Watras *et al.*, 1994). Methyl mercury

is produced in lake systems by methylation of Hg[II]. This process is usually bacterially mediated and occurs mostly in organic-rich compartments of aquatic ecosystems such as sediments, organic nutrients in the water column and periphyton communities (Eisler, 2006; Xun, Campbell & Rudd, 1987). A small amount of methylation also occurs within the gastrointestinal tract and on the external slime layer of fish (Rudd, Furutani & Turner, 1980; McKone, Young, Bache & Lisk, 1971).

Once Hg[II] is in lake water, it can be reduced to elemental Hg^0, methylated in the water column to form methyl mercury, or buried in sediment (Winfrey & Rudd, 1989; Porcella, 1994; Houck & Cech, 2004). Hg^0 that forms in lake water is eventually lost to the atmosphere via evasion (Winfrey & Rudd, 1989). Once methyl mercury has formed in the water column it is available for intake by lake biota and some will be bioaccumulated by organisms at the bottom of the food web and then biomagnified up the food web. Methyl mercury that does not enter the food web will either be further methylated to dimethylmercury (CH_3HgCH_3) which is quickly released from lakes (Winfrey & Rudd, 1989), or will be demethylated to form Hg^0 and methane (Begley, Walts & Walsh, 1986). Finally, Hg[II] that is buried in sediment can be methylated to form methyl mercury which can be released into the lake water and is again bioavailable (Matilainen, Verta, Niemi & Uusi-Rauva, 1991). In addition to atmospheric deposition, methyl mercury can enter lakes directly through water runoff from terrestrial environments and watersheds (Verta *et al.*, 1995; Hultberg, Iverfeldt & Lee, 1994). Methyl mercury is also removed from lakes via tributaries and ground water.

Methyl mercury production in lake water can be affected by environmental fac-

tors including water temperature, pH, lake anoxia, and availability of biodegradable organic carbon (Korthals & Winfrey, 1987; Watras *et al.*, 1994; Verta *et al.*, 1994; Xun *et al.*, 1987). Studies have shown that methyl mercury production is significantly faster in acidic lakes than in higher pH lakes (Xun *et al.*, 1987). Furthermore, methyl mercury production increases with higher temperature and higher levels of biodegradable organic carbon (Korthals & Winfrey, 1987, Watras *et al.*, 1994, Wright & Hamilton, 1982), and is higher in anoxic conditions than when oxygen is present (Verta *et al.*, 1994). Demethylation rates also change depending on pH, temperature and organic carbon but the effects are often smaller (Xun *et al.*, 1987; Verta *et al.*, 1994; Miskimmin, 1989).

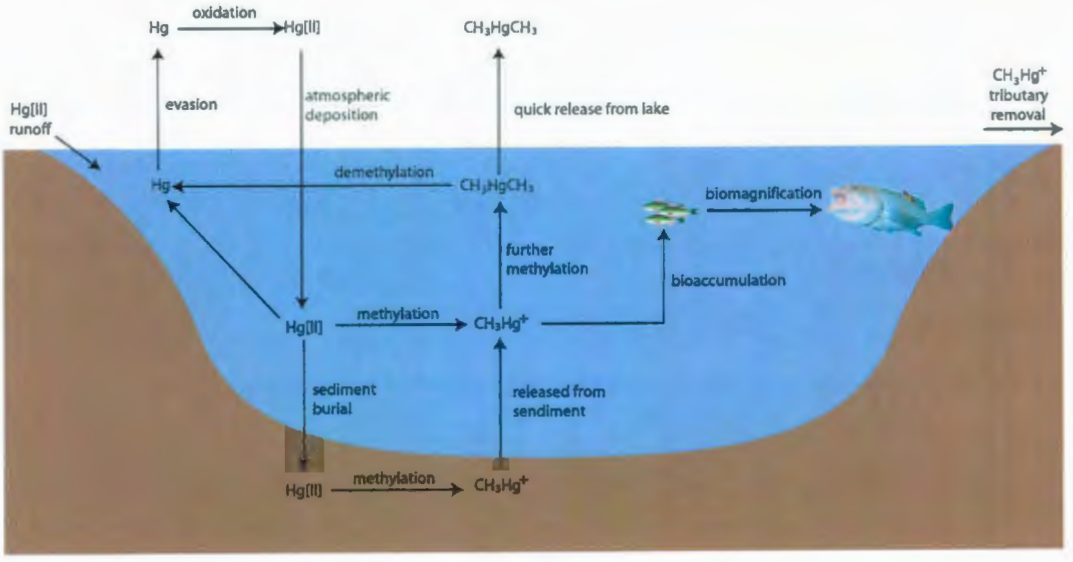


Figure 1.1: The mercury cycle

1.3 Mercury in fish

Methyl mercury is biomagnified through the food web (Beckvar, Field, Salazar & Hoff, 1996). This means that methyl mercury concentration increases with increasing trophic position. Methyl mercury in lakes and streams can be absorbed or ingested by organisms at the base of the food chain. This methyl mercury can then be transferred up through the aquatic food web into top predator fish. As a result, piscivorous fish are exposed to higher concentrations of methyl mercury than fish that feed on lower trophic organisms such as invertebrates.

The majority of mercury entering lake systems is in an inorganic form (Watras *et al.*, 1994). Once inorganic mercury is deposited into a lake it can be converted to methyl mercury by microorganisms, primarily anaerobic bacteria (Compeau & Bartha, 1985). Methyl mercury can be taken in by aquatic organisms either directly from water via gill membranes during respiration, or through food sources (de Freitas, Gidney, McKimmon & Norstrom, 1975; Sarica *et al.*, 2004; Hall, Bodaly, Fudge. Rudd & Rosenberg, 1996) with the majority ($> 90\%$) coming from food sources (Beckvar *et al.*, 1996; Hall *et al.*, 1996). While both inorganic mercury and methyl mercury can be taken in by aquatic organisms, methyl mercury is accumulated more quickly because it has a much slower depuration rate. As a result, approximately 95% of mercury contained in fish is methyl mercury (Bloom, 1992). For this reason, and because of methyl mercury's associated toxic effects, this is the form of mercury that we are concerned with in this study.

Methyl mercury accumulation can be affected by diet. Fish undergo dietary

changes due to season, habitat change, and life history development. These changes can affect methyl mercury exposure and accumulation. Lake temperature and season affect accumulation rates directly by changing fish metabolic rate, and indirectly by influencing methylation rates which alter methyl mercury availability (Verta *et al.*, 1994).

The fish that humans eat are typically the top predators. Top predator fish contain the most methyl mercury due to biomagnification. For this reason, methyl mercury contained in fish can be a serious health concern. Health Canada's guideline for maximum mercury content in commercial marine and freshwater fish is 0.5 parts per million (ppm). While fish are considered a healthy food choice because they are high in protein and low in saturated fat, certain fish species consumed in Canada are known to exceed the 0.5 ppm guideline. As a result, the Canadian Food Inspection Agency has advised consumers, especially pregnant women and children, to limit the consumption of certain fish due to methyl mercury content (Health Canada, 2002).

1.4 Mercury in Labrador

Elevated levels of mercury in Canadian lakes is a recognized problem. Across the country, fish have been found containing methyl mercury levels exceeding the recommended guideline of 0.5 ppm set by Health Canada (Anderson, Scruton, Williams & Payne, 1995; Drysdale, Burgess, d'Entremont, Carter & Brun, 2005; Weech, Scheuhammer, Elliott & Cheng, 2004). This is particularly a concern for communities that consume fish on a regular basis. The Innu population in Labrador is one

such group of people. The Innu people consume fish from local lakes almost daily (Laura Atikessé, personal communication, March 11, 2008).

Figure 1.2: Labrador study lakes

The work in this thesis focuses on four Boreal forest lakes in Labrador. In consultation with the Innu, these lakes were chosen due to frequent food fish harvesting. The properties of these lakes are typical of the hundreds of thousands of Boreal forest lakes in Canada. The lake characteristics and native fish species are presented in Table 1.1 and lake locations are shown in Figure 1.2. There are no point sources of mercury pollution nearby, yet some fish from these lakes were found to contain elevated levels of mercury (Roux, 2008). This poses an increased health risk to frequent fish consumers (like the Innu), thus establishing a need for long-term research

Name	Lake area (km^2)	pH	Location	Native Fish Species
No Name Lake	27.43	5.8	52°41'N,59°24'W	brook trout, longnose sucker, northern pike and white sucker
Rocky Pond	6.21	5.9	52°46'N,59°35'W	brook trout, longnose sucker, northern pike and white sucker
Shipiskan	17.21	6.3	54°39'N,62°24'W	lake trout, longnose sucker, northern pike and whitefish
Panch	20.65	6.0	53°15'N,59°04'W	brook trout, longnose sucker, northern pike. Atlantic salmon, white sucker

Table 1.1: Lake characteristics and native fish species

on mercury contamination and the consequence for human health.

1.4.1 Native fish species

All fish described in this section are harvested and eaten by the Innu year-round. The information provided was taken from Scott and Crossman (1973) unless otherwise noted.

Northern pike (*Esox lucius*) are native to all the study lakes. Northern pike are a large, long-lived fish species that have been reported to live up to 30 years, and to grow well over 1 m long. Adult pike are classed as omnivorous carnivores because they will eat any living vertebrate that they can get their jaws around.

Lake trout (*Salvelinus namaycush*) are native to many lakes in Labrador, but were caught in only one of the study lakes. The lake trout is one of the world's largest

freshwater fish and can grow to well over a metre in length (Ryan, 1988). This is a long-lived fish that often lives 15 to 25 years. The lake trout is a top predator in the study lakes and prefers to eat fish but will eat other food if necessary, including aquatic and terrestrial insects, freshwater sponges, and small mammals.

Brook trout (*Salvelinus fontinalis*), one of the most popular game fish in eastern Canada, were caught in three of the four study lakes. They are carnivorous and eat a variety of food including plankton, insects, worms, snails, mice and some fish with prey size increasing with size of trout (Ryan, 1988). Brook trout are much smaller than northern pike, growing to an average length of 25-30 centimetres, and are typically short-lived (< 5 years). Brook trout are preyed upon by the top predator fish in the study lakes.

The white sucker (*Catostomos comersonii*) was found in three of the four study lakes. These fish are bottom feeders that are only moderately active in the daytime with active feeding taking place near sunrise and sunset. The diet of this fish consists primarily of chironomids, trichoptera, and mollusks. The white sucker is a food item for top predator fish in the study lakes.

The longnose sucker (*Catostomos catostomos*) was found in all the study lakes. This fish is a bottom feeder and feeds exclusively on benthic invertebrates including amphipods, trichoptera, and gastropods. This fish is preyed upon by top predator fish in the study lakes.

The Atlantic salmon (*Salmo salar*) is native to the basin of the North Atlantic Ocean. It is found throughout Newfoundland and Labrador but was caught in only one of the study lakes. The Atlantic salmon is an anadromous fish, however, a number

of populations throughout Newfoundland and Labrador are landlocked, including the salmon in this study. Salmon typically feed upon aquatic insect larvae of chironomids, mayflies, caddisflies, blackflies, and stoneflies, as well as some terrestrial insects. The Atlantic salmon is well-known around the world as both a game fish and a commercial species. The salmon population in the Labrador study lake is preyed upon by northern pike.

Lake whitefish (*Coregonus clupeaformis*) are native to many lakes in Labrador but were caught in only one of the study lakes. Lake whitefish are a cool water species and a bottom feeder, consuming a variety of aquatic insect larvae, mollusks, and amphipods. The lake whitefish is one of the most valuable commercial freshwater fish in Canada and are preyed on by top predator fish in the study lakes.

Chapter 2

Modeling with dynamical systems

Dynamical systems models are useful tools for studying complex systems that change over time. Ordinary differential equations (ODEs) describing system behaviour are used to show the evolution of the system over time. ODEs can sometimes be solved (*e.g.*, if they are linear) but usually are too complex to solve explicitly. In the latter case, dynamical system techniques are used to obtain information about the solution without actually solving the system explicitly. Dynamical systems techniques can be used to make predictions about future activity and performance of systems under various scenarios and to show long-term behaviour. Because biological systems typically involve complicated interactions beyond simple proportionality between components, they are said to be fundamentally nonlinear; a nonlinear ODE model and a dynamical systems solution approach is ideal for the analysis of such systems. A Boreal lake containing mercury can be modeled as a dynamical system of several interacting variables including fish biomass, fish mercury content, and lake mercury content. The

state of the system at time t is given by the value of the system variables at time t.

In order to use differential equations to investigate biological problems, it is first necessary to translate the physical situation into mathematical terms. This is done by making assumptions about the system's behaviour based on observations and other known mechanisms. In this case, observed interactions between fish populations and mercury flux between system compartments were used to construct the model equations. The interactions between the variables in the system are more complicated than that of simple proportionality, thus, the model equations are nonlinear.

Our goal is to capture the essential workings of a system, using the fewest possible rate constants (parameters) which must be known *a priori* for the model.

Once the model has been constructed, analysis of the differential equations begins. Nonlinear equations are not usually solved in a straightforward way and exact solutions cannot be determined in general. For this reason, analysis of nonlinear dynamical systems typically involves using mathematical techniques to determine qualitative information about, or properties of, the solution without actually solving the equations. This is known as the dynamical systems approach.

In this study, system analysis involves determining the stability of the system in the neighbourhood of the fixed points (steady state solutions) according to the following protocol:

- locate the fixed points of the system
- linearize the system in the neighbourhoods of the fixed points
- determine the eigenvalues of the resulting linearized equations to assess the

stabilities of the fixed points

Further analysis performed in this study involves phase portrait analysis of the system to determine qualitative trajectory behaviour and bifurcation analysis to assess system behaviour change when selected system parameters are varied. *Maple* software is used to determine all fixed points and eigenvalues. The remainder of this chapter provides background information necessary for understanding the mathematical analysis used in this study. An introductory text on dynamical systems theory such as Boyce and DiPrima (2005) or Strogatz (2001) will provide more details.

2.1 Fixed points of a system

A fixed point is a location in phase space where the system state is motionless. Phase space is the set of all possible states of the system. The path in phase space that a dynamical system solution follows is called an orbit or phase trajectory. An orbit begins at an initial point and has an orientation consistent with increasing values of time. A fixed point is a type of orbit that is just one point in phase space as the system changes with time. Fixed points represent equilibrium solutions, also known as steady state solutions. In the current study, the value of the system variables (*i.e.*, fish biomass, fish mercury content, and lake mercury content) will be constant at the fixed point, even though mercury is still entering and leaving the lake, and fish are still reproducing and dying.

Definition *Consider the nonlinear system of ordinary differential equations*

$$\frac{dx_i}{dt} = f_i(\mathbf{x}), \tag{2.1}$$

for i=1,...,n

where f_i are non-linear functions of $\mathbf{x}$, *and* $\mathbf{x} = (x_1, ..., x_n)$.

A fixed point $\overline{x} \in \mathbb{R}^n$ *is a point for which*

$$f_i(\overline{x}) = 0 \tag{2.2}$$

for all i=1,...,n

In other words, the point $\overline{x}$ corresponds to a solution at which the system does not undergo any change.

A fixed point (or equilibrium) is said to be stable if all sufficiently small disturbances damp out in time. Otherwise, it is said to be unstable.

Definition *A fixed point* $\overline{x}$ *is said to be stable if, given* $\epsilon > 0$, *there is a* $\delta > 0$ *such that every solution* $x = \phi(t)$ *of the system (2.1) which at* $t = 0$ *satisfies* $|\phi(0) - \overline{x}| < \delta$ *exists and satisfies* $|\phi(t) - \overline{x}| < \epsilon$ *for all* $t \geq 0$. *A fixed point that is not stable is said to be unstable.*

In other words, if $\overline{x}$ is a stable fixed point, then all solutions that start sufficiently close (within the distance δ) to $\overline{x}$ stay close (within the distance ϵ).

Definition *A fixed point* $\overline{x}$ *is said to be asymptotically stable if it is stable and, in addition,* $|\phi(t) - \overline{x} \rightarrow 0$ *as* $t \rightarrow \infty$.

If $\overline{x}$ is an asymptotically stable fixed point, then all solutions that start sufficiently close to $\overline{x}$ will approach $\overline{x}$.

In the model analysis in Chapter 4, fixed points denoted as "stable" may be technically referred to as "asymptotically stable".

Eigenvalue analysis can be performed to determine the stability property of typical fixed points. In order to do this, an understanding of linear algebra techniques and ideas is required.

2.2 Linear systems of ODEs

A system of n simultaneous linear algebraic equations in n variables,

$$a_{11}x_1 + a_{12}x_2 + ... + a_{1n}x_n = b_1$$
$$\vdots \qquad\qquad \vdots$$
$$a_{n1}x_1 + a_{n2}x_2 + ... + a_{nn}x_n = b_n$$

can be written as

$$\mathbf{Ax} = \mathbf{b}$$

where the n x n matrix $\mathbf{A}$ and the vector $\mathbf{b}$ are given, and the components of $\mathbf{x}$ are to be determined.

The equation

$$\mathbf{Ax} = \mathbf{b}$$

can be viewed as a linear transformation that transforms a given vector $\mathbf{x}$ to a given vector $\mathbf{b}$. To find such vectors we set $\mathbf{b} = \lambda X$, where λ is a scalar proportionality factor. We then seek solutions of the equations

$$\mathbf{Ax} = \lambda \mathbf{X}$$

or

$$(\mathbf{A} - \lambda\mathbf{I})\mathbf{x} = 0$$

where $\mathbf{I}$ is the identity matrix. The latter equation has nonzero solutions if and only if λ is chosen so that $det(\mathbf{A} - \lambda\mathbf{I}) = 0$. This equation is called the characteristic equation and values of λ that satisfy this equation are called eigenvalues of the matrix $\mathbf{A}$. In other words, the eigenvalues of $\mathbf{A}$ are the roots of the characteristic equation.

The eigenvalue problem for systems of linear algebraic equations is related to solutions of linear differential equations. Solutions of linear differential equations can be determined using the eigenvalue problem for algebraic equations as follows.

A system of n linear differential equations

$$\dot{x}_1 = a_{11}(t)x_1 + a_{12}(t)x_2 + ... + a_{1n}(t)x_n$$

$$\vdots \qquad\qquad\qquad\qquad \vdots$$

$$\dot{x}_n = a_{n1}(t)x_1 + a_{n2}(t)x_2 + ... + a_{nn}(t)x_n$$

can be written in matrix notation as

$$\dot{\mathbf{x}} = \mathbf{A}(t)\mathbf{x} \tag{2.3}$$

where $x_1 = \phi_1(t), ..., x_n = \phi_n(t)$ are the components of the vector $\mathbf{x} = \phi(t)$ and $a_{11}(t), ..., a_{nn}(t)$ are the elements of an n x n matrix $\mathbf{A}(t)$. The eigenvalues of a matrix $\mathbf{A}$ can be used to find solutions for differential equations whereby system 2.3 has solution $\mathbf{x}(t) = e^{\lambda t}\mathbf{v}$ if and only if, for the matrix $\mathbf{A}$, λ is an eigenvalue and $\mathbf{v}$ its corresponding eigenvector.

2.3 Analysing systems of nonlinear ODEs

A system of nonlinear ODEs may have several fixed points. For nonlinear systems there is often no way to calculate explicit solutions so we instead try to determine the qualitative behaviour of the solutions. Near the fixed point, a typical nonlinear system behaves like a linear system and can be approximated by linearized equations. Linearizing about a fixed point gives a more qualitative measure of stability.

System behaviour can be graphically represented using a phase portrait. A phase portrait is a pictorial view in phase space showing fixed points and all the qualitatively different orbits of the system. Figure 2.1 is an example of a phase portrait. This phase portrait shows one (asymptotically) stable fixed point with an orbit spiralling inward towards it.

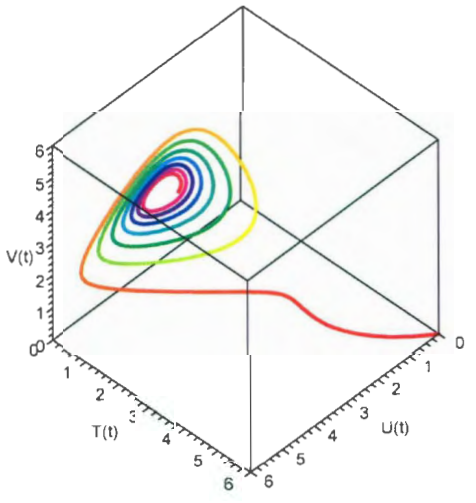


Figure 2.1: Phase portrait

2.4 Stability of a fixed point

Linearizing a set of nonlinear equations about a fixed point provides insight to local behaviour. Stability properties of the fixed point can be found by studying the eigenvalues of the linearized system. Eigenvalues associated with a fixed point can either be real or complex. In the case of real eigenvalues, if one or more eigenvalues are positive the solution is unstable and will move away from the fixed point with time. When all eigenvalues are negative, the solution is stable and tends toward the fixed point with time. Complex eigenvalues cause oscillatory behaviour of the system solution. In the case of complex eigenvalues, the fixed point is stable when the real parts of the eigenvalues are negative, and is unstable otherwise. Oscillations decay over time if the fixed point is stable, and grow over time if the fixed point is unstable. The frequency of the oscillations is determined by the complex part of the eigenvalues.

When a fixed point is (asymptotically) stable, all solutions starting near the fixed point approach it as $t \to \infty$. When a fixed point is unstable (*i.e.*, one or more eigenvalues have positive real parts) some or all solutions starting near the fixed point will move away from it as $t \to \infty$. Thus, the stability of a given fixed point can be determined from direct inspection of the eigenvalues.

2.5 Bifurcation analysis

Bifurcation theory involves studying changes in the qualitative structure of solutions of differential equations as parameters are varied. Often when parameter values are varied there is no qualitative change in system behaviour. However, sometimes just

a slight change to a parameter value results in major changes to system behaviour including fixed point creation or destruction, or fixed point stability changes. These qualitative changes in system dynamics are called bifurcations and the values where they occur are bifurcation points.

Bifurcation analysis is a useful tool that provides information regarding system behaviour even when parameter values are not known precisely. It is also used to show how sensitive the model is to variations in values of the parameters. System behaviour changes resulting from bifurcations can be shown graphically using a bifurcation diagram. A bifurcation diagram is a graphical depiction of locations and stability properties of fixed point solutions as a function of a parameter. Fixed point stability is shown on the bifurcation diagram by using a solid curve for stable solutions and a dotted curve for unstable solutions (see Figure 2.2).

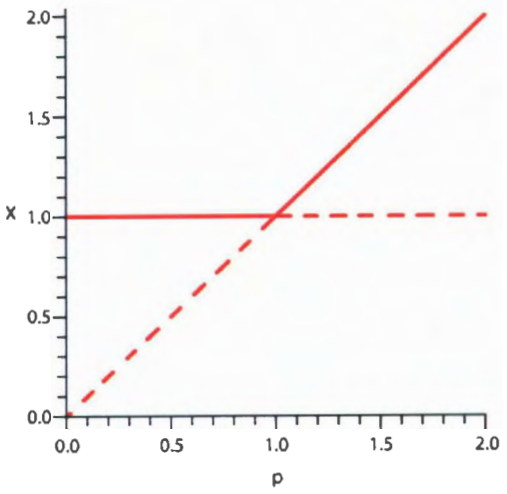


Figure 2.2: Bifurcation diagram showing a transcritical bifurcation

There are different types of bifurcations which result in different types of changes to system behaviour. The type of bifurcation observed in this paper is a transcritical bifurcation. Transcritical bifurcations occur when two fixed points intersect and exchange their stability properties. In this model, we see that slight perturbations to the harvesting parameter cause an exchange in stability between two fixed points whereby a fixed point that was stable becomes unstable and simultaneously a previously unstable fixed point becomes stable. Figure 2.2 is an example of a bifurcation diagram showing a transcritical bifurcation. The phase space variable is X and the bifurcation parameter is p. Figure 2.2 shows an exchange of stability at $(p, X) = (1, 1)$ where two fixed point solutions intersect and exchange stability.

In this study two models are analysed. The first illustrates the situation of methyl mercury moving between a single fish species and the lake, and the second considers methyl mercury moving between two species of fish and the lake, as well as the predator-prey dynamics between the fish species. The model analysis for each model is as follows:

1. Solve the system for fixed points.
2. Determine fixed point stability using eigenvalue analysis.
3. Generate phase portraits to show orbits from different initial conditions.
4. Plot numerical solutions of system variables with respect to time.
5. Generate bifurcation diagrams to show changes in fixed point solutions as a control parameter is varied.

6. Change model to incorporate seasonal (periodic) behaviour of certain parameters.

7. Re-generate phase diagrams to show seasonal effect on the orbits.

8. Re-generate numerical solutions with respect to time to show seasonal effect.

Dynamical systems theory is applied differently in the case of seasonal (periodic) parameters because the ODE system in this case is nonautonomous. The geometric qualitative analysis discussed in this chapter cannot be effectively extended to nonautonomous systems because the concepts of fixed point and stability are less straightforward. In order to apply dynamical systems theory to nonautonomous systems Floquet Theory is required, which is beyond the scope of this thesis.

Chapter 3

The models

Two models are developed here to show methyl mercury movement between lake water and fish populations. These models incorporate necessary biological and chemical processes.

The first model is a single-species model that analyses methyl mercury movement between a lake and a single fish population. The second model is a predator-prey model that analyses methyl mercury movement between predator and prey fish populations as well as between the lake and the fish populations. This model shows the predator-prey population dynamics as well as the methyl mercury flux.

To our knowledge, these are the first dynamical systems models constructed to predict the effect of a non-lethal toxicant on biological populations.

3.1 Single-species model

The single-species model is 3-dimensional. It describes the biomass of the fish population (X) occupying the highest trophic position, and the interactions between methyl mercury in the lake water (T) and in the fish population (U). System variables are listed in Table 3.1 along with a description and units.

There are several assumptions involved with this model. Firstly, in this model we are only concerned with average, adult fish. This means juvenile fish are not considered. Since we are only concerned with average, adult fish, we ignore any effects related to biodilution (fast-growing fish accumulating less mercury). Further, some studies have also shown that in certain fish, mercury is accumulated greater in the early years (Edwards, Trudel & Mazumder, 2005). However, we do not consider age-related changes in methyl mercury accumulation explicitly in the model because we are not looking at individual fish but, rather, we are concerned with the total biomass in a cross-section of time.

Secondly, in this model we are assuming that the reproduction rate is unaffected by methyl mercury in the population. We make this assumption because, although there have been some studies showing a negative effect on reproduction with mercury exposure (Heisinger & Green, 1975), these studies were performed in water containing unrealistically high mercury concentrations (between 10-40mg/L mercuric chloride, 1.8mg/L methyl mercury).

Furthermore, we assume rates of mercury methylation and accumulation are the same throughout the lake. That is, we do not explicitly consider differences in methy-

Variable	Description	Units
X	Biomass of population	tonnes fish·km^{-2}
T	Amount of methyl mercury in lake water	grams MeHg·km^{-2}
U	Amount of methyl mercury contained in the population	grams MeHg·km^{-2}

Table 3.1: Single-species model variables

lation rates and accumulation rates that exist between lake pelagic zones and littoral zones.

Finally, we assume that fish can directly re-absorb mercury that has been excreted when, in actual fact, the pathway is more complicated. Mercury is excreted from fish as inorganic mercury so before fish can accumulate this mercury again, it must be methylated. Thus, the time delay which occurs between the time mercury is lost from the fish and when it is again available for uptake is ignored.

The model is as follows:

$$\dot{X} = rX\left(1 - \frac{X}{k}\right) - h_1 X$$

$$\dot{T} = -dT + g_1 U + f - aXT$$

$$\dot{U} = aXT - g_1 U - p_1 h_1 U$$

Here, $\dot{X}$ denotes $\dot{X} = \frac{dX}{dt}$, the rate of change of the population at time t, where t is measured in years.

3.1.1 Description of model terms

The terms in the model are described in the following subsections.

Equation 1 – Population biomass

The first equation represents population biomass (X). This equation describes growth of a typical single-species population that is regulated by density-dependant factors such as limitations of food supply (Hastings, 1997). It is comprised of three terms: one term to account for growth and two terms to account for population loss. The first term represents population growth where r is the intrinsic growth rate. The second term represents the restriction put on population growth due to the carrying capacity of the surrounding environment, k. The third term in the equation represents the death rate of the population due to harvesting by humans, where h_1 is the rate of harvesting. There is no parameter in this equation for natural death rate because it has been reported that in our study lakes there is very little natural death – the fish in these lakes are long-lived fish that are eventually harvested. If the situation changed in such a way that natural deaths were occurring, an adjustment to the estimated value of h_1 would be required such that h_1 = harvesting rate + natural death rate.

Equation 2 – Methyl mercury in water

The second equation represents the total methyl mercury in the lake water (T). This equation is composed of four terms: two for methyl mercury removal and two for methyl mercury input. The first term represents methyl mercury that is removed from the lake through natural processes, where d is the rate at which methyl mercury is removed via sediment burial and demethylation. The second term represents methyl mercury that is transferred from fish into the lake through excretion. Methyl

mercury is eliminated from fish through an exponential decay process where g_1 is the rate of methyl mercury excretion and is obtained from analysis of half-life measures. The term f is the rate methyl mercury is input to the lake via direct deposition, methylation in the water column, and from sediment. The final term represents methyl mercury that is removed from the lake due to uptake by lake biota. The parameter a is the rate that methyl mercury is taken in by the fish via the food web.

In this model we make the simplifying assumption that all parameters are constant rates. In a realistic setting, however, the parameters f and d vary depending on season. In this thesis, seasonal effects on these parameters are discussed in section 4.4.1.

Equation 3 – Methyl mercury in fish

The third equation represents the total methyl mercury contained in the fish population (U). This equation is comprised of three terms: one for methyl mercury input and two for methyl mercury removal. The first term represents methyl mercury that enters the fish population via the food web where a is the rate that methyl mercury is bioaccumulated through the food web. The second term represents methyl mercury removed from the population via excretion, this term is necessary to maintain mass-balance in the system. The final term represents methyl mercury that is removed as a result of harvesting where h_1 is the harvesting rate and p_1 is the relative size of harvested fish compared with the general population. The parameter p_1 adjusts the amount of methyl mercury removed based on the size of fish that are typically harvested.

3.1.2 Description of model parameters

This model contains eight parameters which are rate constants for various aspects of the system. A description of each parameter is given in Table 3.2, along with units; the estimated parameter values used in this thesis can be found in Table 3.3. This section provides information related to the meaning and significance of each parameter, and how the parameter value was obtained. Values of the rate constants for the study lakes were unavailable. However, a literature review provided values for several rate constants in other lakes with similar characteristics including native fish species, lake process behaviour, temperature, size, depth and pH. Parameter values related to mercury contamination processes were abundant in the literature but many parameters related to population biology were not as readily available.

The parameter r is the intrinsic growth rate of the fish population. This is the growth rate in the absence of any limiting factors. In the absence of density-dependent effects, if $r > 0$, the population grows exponentially, if $r < 0$ the population decays exponentially, and if $r = 0$ the population is stationary. There was no data available for the intrinsic growth rates of the fish populations in the study lakes so the value of $r = 2$ was chosen for the purpose of this study.

The parameter k is the carrying capacity of the fish population. This parameter restricts population growth based on the carrying capacity of the surrounding environment. Estimating this parameter can be difficult because there is often very little information available to quantify what size population a lake can support. The fish populations in the Labrador study lakes are relatively undisturbed since there is no

known disease and the rate of harvesting is small. For this reason, it is likely that the fish populations in these lakes are at, or very near, their carrying capacity. This means that a current biomass estimate can be used to approximate the value for k. The population biomass for our study lakes was estimated from biomass data for other similar northern lakes. Values for fish biomass range greatly from < 10 kg·ha^{-1} up to > 300 kg·ha^{-1} in northern lakes (Blumenshine, Lodge & Hodgson, 2000; Trippel & Harvey, 1986; Rask & Arvola, 1985; Hanson & Leggett, 1982). Hanson and Leggett (1982) performed a literature review and reported on 20 lakes and ponds with various surface area, mean depth and geographic distribution. Biomass estimates for a significant portion of these lakes falls within the range of 100-400 kg·ha^{-1} so the value of $k = 200$ kg·ha^{-1} (or 20 tonnes·km^{-2}) was chosen for this study.

The mercury elimination parameter g_1, is the rate that methyl mercury is removed from the population via excretion. The process of methyl mercury elimination from fish is biphasic: the first, fast-clearing component represents the portion of ingested methyl mercury that is not absorbed by the epithelium and has a half-life of days to weeks, while the second, slow-clearing component consists of methyl mercury mainly associated with muscle tissue and has a half-life of months to years (de Freitas *et al.*, 1975; Ruohtula & Miettinen, 1975; Jarvenpaa, Tillander & Miettinen, 1970). The majority of ingested methyl mercury (70-80%) is eliminated via the second, slow component when fish are given a single dose of mercury. Further, it has been suggested that fish which are chronically exposed to methyl mercury excrete it almost exclusively from the slow component (Kramer & Neidhart, 1975). For this reason, we only consider the second, slow-clearing component of methyl mercury elimination in

this model.

The value of $g_1 = 0.42$ was calculated based on a half-life for methyl mercury elimination of 2 years (Ruohtula & Miettinen, 1975; Miettinen, Tillander, Rissanen, Miettinen & Ohmomo, 1969; Jarvenpaa *et al.*, 1970). Calculations can be found in Appendix 6.1.1.

There is no published data regarding harvesting rates in our study lakes. To compensate for this, a numerical sensitivity analysis was performed on the harvesting parameters. This analysis demonstrated that the model results are not sensitive to the harvesting parameter value as long as the harvesting rate does not exceed the population growth rate (r), which is the case in the study lakes. Of course, if the harvesting rate is larger than the intrinsic growth rate, the population will tend to extinction over time. It is known that the harvesting parameters are greater than zero (since some harvesting occurs) but less than one (since harvesting rates are fairly low in the area), so the value $h_1 = 0.6$ was chosen.

The parameter p_1 indicates the relative size of the harvested fish compared with the general fish population. Fish that are harvested tend to be of average size or greater since smaller fish avoid nets or escape from nets more often and fishers target larger fish. Studies have shown that older and larger fish contain more mercury (Drysdale *et al.*, 2005). If it were always average size fish that were harvested the value of p_1 would be 1. In our case, a value of $p_1 = 1.2$ was chosen because the harvested fish tend to be of greater than average size.

The parameter f is the rate that methyl mercury is input to the lake. Some methyl mercury enters the lake system through runoff, wetland drainage and directly from

the atmosphere, while the majority is a result of within-lake methylation of inorganic mercury (Hg[II]). Hg[II] is methylated in the water column, in lake sediment, and in the intestines and external slime layer of fish (McKone *et al.*, 1971; Rudd *et al.*, 1980). Methyl mercury released from the sediment is likely produced in the top layers of sediment since most of the methyl mercury produced in deeper sediments is destroyed through demethylation processes before it can reach the sediment surface and be released into the lake (Wright & Hamilton, 1982).

The value of f was estimated based on studies performed in other northern lake systems. Rate of methyl mercury input from the sediment layer was estimated to be 5.4g MeHg·km^{-2}·yr^{-1} based on measured values from Clay Lake, Ontario (Wright & Hamilton, 1982). Methyl mercury input from direct atmospheric deposition was estimated to be 0.1 g MeHg·km^{-2}·yr^{-1} based on Verta *et al.*'s (1994) measurement of Boreal lakes in southern Finland. The value of f = 5.5 g MeHg·km^{-2}·yr^{-1} was obtained by summing the individual methyl mercury input rates. I was unable to find suitable data pertaining to methylation rate within the water column. While Xun *et al.* (1987) obtained measurements of this rate, the methods used do not measure natural rates of methylation activity but, rather, provide rates under experimentally manipulated settings (*i.e.*, varied pH, mercury concentration, etc). Most studies suggest that methylation rates in the water column are low (Eckley & Hintelmann, 2006; Lucotte, 1999). Consequently, mercury methylation within the water column is not a component of the estimated value for f in this model. Furthermore, methyl mercury produced within the gastrointestinal tract and on the external slime layer of fish is considered insignificant compared with other inputs (Hall *et al.*, 1996) and

was not considered when calculating f.

Mercury methylation is a seasonal process that is affected by temperature (Winfrey & Rudd, 1989; Verta *et al.*, 1994) whereby methylation rates peak in the summer and are lower throughout the remainder of the year. The seasonal effect on f is discussed in section 3.3.1.

The parameter d is the rate that methyl mercury is removed from the lake system. Methyl mercury is removed from the lake system by a variety of processes including demethylation in the water column, sediment burial, and tributary outflow. A significant amount of mercury is also lost through atmospheric evasion (*i.e.*, evaporation) but this involves elemental mercury (Hg^0) only so it is not included here (Fitzgerald *et al.*, 1994; Watras *et al.*, 1994; Cooke, 2002). In the water column, demethylation rates are much smaller than methylation rates (Xun *et al.*, 1987) and, for this reason, demethylation in the water column was not considered when estimating d. In order to estimate a value for methyl mercury removed through sediment burial, Watras *et al.*'s (1994) data for Wisconsin lakes (measured in terms of methyl mercury lost annually per lake area) were applied to the Labrador lakes to obtain a value of 0.27year^{-1}. Thus, the rate of methyl mercury removed from the lake system was estimated to be $d = 0.3\text{year}^{-1}$ (calculations can be found in Appendix 6.1.2).

The parameter a is the rate methyl mercury enters the fish population through the food web. While some methyl mercury accumulates in fish directly from water during respiration, the majority ($> 85\%$) is obtained through food sources (Hall *et al.*, 1996). We are using the simplifying assumption that methyl mercury accumulates in the fish population at the rate of a so that

Parameter	Description	Units
r	Intrinsic growth rate of population	year^{-1}
k	Carrying capacity of the environment	tonne fish$\cdot\text{km}^{-2}$
h_1	Rate of fish harvesting (effort harvesting)	year^{-1}
d	Rate methyl mercury removed from lake	year^{-1}
g_1	Rate mercury is eliminated from fish naturally	year^{-1}
f	Rate of methyl mercury input to lake	g MeHg$\cdot\text{km}^{-2}\cdot\text{year}^{-1}$
a	Rate methyl mercury bioaccumulated through the food web	$\text{km}^2\cdot\text{tonne}^{-1}$ fish$\cdot\text{year}^{-1}$
p_1	Relative size of harvested fish to general fish population	no units

Table 3.2: Single-species model parameters

Parameter	Estimated Value	Reference
r	2	Estimated by author
k	20	Hanson and Leggett, 1982
h_1	0.6	Estimated by author
d	0.3	Watras *et al.*, 1994
g_1	0.42	Miettinen *et al.*, 1969
f	5.5	Wright and Hamilton (1982); Verta *et al.* (1995)
a	0.1	Estimated by author
p_1	1.2	Estimated by author

Table 3.3: Single-species model parameter values

- the model can be applied to lakes where trophic structure of the fish populations is unknown
- the model does not require a separate biomass and methyl mercury equation for each trophic level.

If the model did include separate biomass and methyl mercury equations for each trophic level the added complexity would make it very difficult to analyse the model. Further, the model would be less accurate due to an increased number of unknown parameters associated with the extra equations. The time delay for the methyl mercury to make its way through the food web is ignored. For the purpose of this study a was estimated to be 0.1 $km^2 \cdot tonne^{-1}$ $fish \cdot yr^{-1}$.

3.2 Predator-prey model

The predator-prey model is a 5-dimensional model describing fish biomass and mercury flux. The first two equations describe the biomass of the predator (Y) and prey (X) populations, while the last three equations describe methyl mercury movement between lake water and fish (T), and between fish populations (V, U). System variables are listed in Table 3.4 along with variable description and units.

The model is as follows:

$$\dot{X} = rX(1 - \frac{X}{k}) - p_x XY - h_1 X$$

$$\dot{Y} = cp_x XY - h_2 Y$$

$$\dot{T} = -dT + g_1 U + g_2 V + f - aXT + (1 - b)UYp_x$$

Variable	Description	Units
X	Biomass of prey population	tonnes fish·km^{-2}
Y	Biomass of predator population	tonnes fish·km^{-2}
T	Amount of mercury in lake water	grams MeHg·km^{-2}
U	Amount of mercury contained in the prey population	grams MeHg·km^{-2}
V	Amount of mercury contained in the predator population	grams MeHg·km^{-2}

Table 3.4: Predator-prey model variables

$$\dot{U} = aXT - UYp_x - g_1U - p_1h_1U$$

$$\dot{V} = bUYp_x - g_2V - p_2h_2V$$

There are several assumptions involved with this model. All of the assumptions outlined in section 3.1 apply to the predator-prey model. In addition to these, we also assume that the various species of prey fish in the study lakes (see section 1.4.1) behave similarly in terms of population growth rate, carrying capacity and harvesting rates. Further, we assume that both species of predator fish found in the study lakes (northern pike and lake trout) behave similarly in terms of predator functional response, growth efficiency and harvesting rates. Finally, the model ignores any predator-switching behaviour, and assumes prey fish are the sole food source for predator fish.

3.2.1 Description of model terms

The terms of the model are described in the following subsections.

Equation 1 – Prey population biomass

The first equation represents the prey population biomass. This equation describes growth of a typical population that is regulated by density-dependent factors (e.g. limitations of food supply) and predation by other species. It is comprised of four terms: one term to account for growth and three terms to account for population loss. The first term represents population growth where r is the intrinsic growth rate. The second term represents the restriction on population growth due to the carrying capacity of the surrounding environment, k. The third term represents the loss of prey biomass due to predation where p_x is the predator functional response. The fourth term represents the death rate of the population due to harvesting by humans where h_1 is the rate of harvesting. There is no parameter in this equation for natural death rate because it has been reported that there is very little natural death in the study lakes. The fish in these lakes are long-lived fish that are eventually harvested. If the situation were to change such that natural deaths were occurring, an adjustment to the value of h_1 would be required where h_1 = harvesting rate + natural death rate.

Equation 2 – Predator population biomass

The second equation is the Lotka-Volterra equation for predator population biomass. This equation is comprised of two terms: one to account for growth and one to account for loss. The first term represents the increase in predator population as a result of predation on prey where the constant p_x is the rate of predation (or predator functional response). Since only a portion of food consumed by the predator

is converted to predator biomass, the food conversion efficiency is given by c. The second term represents the death rate of the predator population due to harvesting by humans where h_2 is the predator harvesting rate. Like the single-species model, there is no natural death rate based on reports that there is very little natural fish death in the study lakes.

Equation 3 – Methyl mercury in water

The third equation represents the total methyl mercury in the lake water. This equation is composed of six terms: two for mercury removal and four for mercury input. The first term represents methyl mercury that is removed from the lake through natural processes, where d is the rate methyl mercury is removed via sediment burial and demethylation. The second and third terms in this equation represent methyl mercury that is eliminated from the fish populations through excretion, and immediately input to the lake. Methyl mercury is eliminated from fish through an exponential decay process where g_1 and g_2 are the rates of methyl mercury excretion. These parameters were obtained from analysis of the half-life of the exponential decay. The fourth term, f, is the rate methyl mercury is input to the lake via direct deposition, methylation in the water column, and from sediment. The fifth term represents methyl mercury that is removed from the lake due to ingestion by lake biota. The parameter a is the rate that methyl mercury is taken in by the fish via the food web. The sixth and final term represents methyl mercury that is ingested into the predator population via predation (where p_x is the rate of predation) but is not absorbed. The process of methyl mercury assimilation is biphasic in which the first component involves a portion of

ingested methyl mercury being excreted very quickly. The constant b represents the portion of methyl mercury that is assimilated by the fish and, thus, $(1 - b)$ is the amount of methyl mercury that is excreted by the predator fish into the lake during the fast component of assimilation.

It is important to note that the rate of methyl mercury assimilation is much different and greater than biomass assimilation rate (*i.e.*, $b > c$). When food is digested, some of the food energy is required for metabolism, some is excreted, and some is used for growth (Weatherley & Gill, 1987). The parameter c denotes the portion that is used for growth (*i.e.*, the growth efficiency). The rate that methyl mercury is assimilated from food eaten, or the methyl mercury assimilation efficiency from food (b), is quite different. Methyl mercury forms covalent bonds with proteins so b is expected to vary with protein assimilation (Trudel, Tremblay, Schetagne & Rasmussen, 2000). Fish have a high protein requirement for growth and protein can be approximately 70% of fish calories (Weatherley & Gill, 1987, p.28). Methyl mercury assimilation rate is related to the protein assimilation rate but is not directly related to the food conversion efficiency which is why the estimated values of b and c are so different.

Equation 4 – Methyl mercury in prey population

The fourth equation represents the methyl mercury contained in the prey population. This equation is comprised of four terms. The first term represents methyl mercury that enters the fish population via the food web where a is the rate that methyl mercury is bioaccumulated through the food web. The second term is the methyl

mercury that is removed from the prey population as a result of predation (*i.e.*, when a predator eats a prey fish the methyl mercury contained in that fish is no longer in the prey population). The third term is methyl mercury removed from the population via excretion - this term is necessary to maintain mass-balance in the system. The fourth term is the portion of methyl mercury removed from the prey population (and the entire system) due to harvesting, where h_1 is the harvesting rate and p_1 is the relative size of harvested fish compared with the general population.

Equation 5 – Methyl mercury in predator population

The fifth equation represents methyl mercury contained in the predator population. This equation is comprised of three terms. The first term is methyl mercury that is assimilated from the prey population as a result of predation. The second term represents the elimination of methyl mercury from the fish via excretion. The third term is the portion of mercury removed from the predator population (and the entire system) due to harvesting.

3.2.2 Description of parameters

The model contains fourteen parameters which are rate constants for various aspects of the system. Eight of these parameters are the same as in the single-species model (see Section 3.1.2). Units and a description of the additional six parameters are given in Table 3.5. The estimated parameter values used in this thesis can be found in Table 3.6.

In order to analyse the factors influencing rate of resource utilization by predator

Parameter	Description	Units
p_x	Predator functional response; rate of predation	$km^2 \cdot tonne\ fish^{-1} \cdot year^{-1}$
h_2	Harvesting rate for predator population	$year^{-1}$
p_2	Portion of predator population that is harvested	No units
c	Food conversion efficiency	No units
b	Methyl mercury assimilation rate	No units
g_2	Rate methyl mercury is eliminated from predator fish naturally	$year^{-1}$

Table 3.5: Predator-prey model parameters

Parameter	Estimated Value	Reference
p_x	0.3	Estimated by author
h_2	0.6	Estimated by author
p_2	1.2	Estimated by author
c	0.25	Diana, 1979
b	0.8	Trudel *et al.*, 2000
k	25	Hanson and Leggett, 1982
h_1	0.5	Estimated by author

Table 3.6: Predator-prey model parameter values

fish, a Holling Type II predator functional response was considered. Other Holling Types (Type I and III) are a good fit for many models however, Type II functional response was considered here because it describes the feeding rate of predators that spend some time searching for prey and some time processing captured prey (i.e., handling time). The predator functional response was difficult to estimate based on literature data due to its units of $km^2 \cdot tonne\ fish^{-1} \cdot year^{-1}$. There is no data available with rates measured this way. Because of this, the value of p_x was chosen by the author after a sensitivity analysis was performed (see Section 4.2.4 for details). Examination

of the system behaviour using several values of p_x showed that an increase in p_x causes the solutions to have more sustained oscillations and take longer to reach the fixed point. For the purpose of this study a rate of $p_x = 0.3$ was chosen.

In this model, the parameter k represents the carrying capacity of the prey population rather than the predator population. The value was set slightly higher for this model since the carrying capacity tends to be higher for prey populations than predator populations. The value $k = 25$ was chosen based on Hanson and Leggett's (1982) literature review.

As mentioned previously, there is no data available regarding harvesting rates for predator or prey fish populations in the study lakes. To compensate for this, a numerical sensitivity analysis was performed on both h_1 and h_2. The result was that the model is not sensitive to the harvesting rate of the fish populations provided the prey harvesting rate does not exceed the population growth rate (*i.e.*, $r - h_1 > 0$). There is no immediate danger of this happening in the study lakes given the current limited harvesting pressure. As in Section 3.1.2, it is known that the harvesting parameter is between zero and one (since harvesting does occur in the area but at fairly low rates), so the value of $h_1 = 0.5$ and $h_2 = 0.6$ were chosen.

The parameter p_2 indicates the relative size of the harvested predator fish compared with the general fish population. Fish that are harvested tend to be of average size or greater since smaller fish avoid nets or escape from nets more often. Studies have shown that older and larger fish contain more methyl mercury (Drysdale *et al.*, 2005; Weech *et al.*, 2004). If it were always average size fish that were harvested then the value of p_2 would be 1. In our case, a value of $p_2 = 1.2$ was chosen because the

size of harvested fish is often average but sometimes greater than average.

Food conversion efficiency, or growth efficiency, is the conversion of absorbed food into new tissue (Kelso, 1972). Food conversion efficiency for adult northern pike ranges between 0.24 - 0.27 depending on season (Diana, 1979). For the purpose of this model, the rate of $c = 0.25$ was chosen.

Mercury assimilation rates have been reported to range between 70-90% (de Freitas *et al.*, 1977). The value of $b = 0.8$ was chosen in this study based on the reasoning that methyl mercury forms covalent bonds with proteins and, therefore, methyl mercury assimilation is expected to vary with protein assimilation (Trudel *et al.*, 2000). Protein assimilation is approximately 80% in carnivorous fish (Brett and Groves, 1979). The value of $b = 0.8$ also corresponds with results from studies performed on rainbow trout, *(Salmo gairdneri)*, by Rodgers and Beamish (1982) in which mercury assimilation was found to range between 70-80%.

The values for the remaining parameters are the same as in the single-species model (see Table 3.3).

3.3 Seasonal effect on models

A harsh climate causes the Labrador study lakes to freeze for approximately 7-8 months of the year (Scruton, 1984). During this frozen period, the decreased temperatures and ice cover on the lake causes feeding rate (p_r), metabolic processes and mercury processes to slow down. A decrease in metabolic rate causes a change to several of the model rate constants including methyl mercury bioaccumulation (b),

food conversion efficiency (c) and methyl mercury elimination (g_1 and g_2).

In terms of mercury processes, ice cover on the lake prevents methyl mercury from being deposited directly from the atmosphere or through run-off and decreases the amount of methyl mercury leaving the lake system via tributaries. In addition, the decreased lake temperature causes methylation and demethylation processes within the lake to slow down which means less methyl mercury is released from, and buried in, sediment. Overall, methyl mercury input (f) and output (d) rates slow down. In the spring, when temperature increases, snow and ice that has accumulated on the lake surface throughout the winter begins to melt. During this melting period methyl mercury enters the lake at a much higher rate. At the same time, methyl mercury tributary removal rate increases and methylation processes within the lake speed up.

In order to mathematically analyse what effect parameter seasonality has on the system, the models were changed slightly such that the seasonal parameters (b, c, p_x, g_1, g_2, f and d) are multiplied by a periodic function. The function $0.5(\text{sgn}(\sin 2\pi t - 0.5)) + 7/6$ (where sgn refers to the sign of the term; $\text{sgn}(x) = +1$ when x is positive and -1 when x is negative) is a positive function that exhibits periodic behaviour alternating between 0.67 and 1.67 (refer to Figure 3.1). This function ensures that terms containing seasonal parameters are multiplied by 0.67 two thirds of the time (8 months/year) and are multiplied by 1.67 the rest of the time (4 months/year). Incorporating this function in the model this way mimics the effect of seasonal temperature changes and spring snow melt.

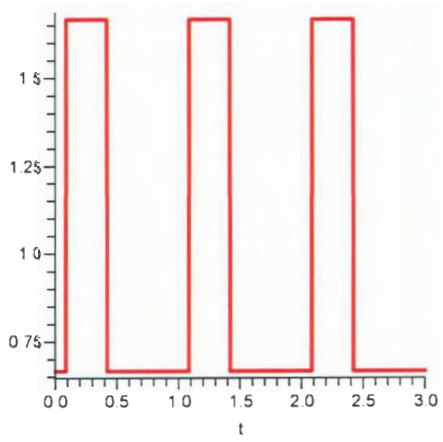


Figure 3.1: Seasonal function

3.3.1 Single-species model with seasonal effects

In order to analyse the effect of seasonal behaviour, the single-species model from Section 3.1 was modified as follows:

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{k}\right) - h_1 X$$

$$\frac{dT}{dt} = -d\Phi T + g_1 \Phi U + f\Phi - aXT$$

$$\frac{dU}{dt} = aXT - g_1 \Phi U - p_1 h_1 U$$

where $\Phi = 0.5(\text{sgn}(\sin 2\pi t - 0.5)) + \frac{7}{6}$

The system equations are identical to the equations in Section 3.1 except that the seasonal parameters are now multiplied by the time-periodic function Φ.

3.3.2 Predator-prey model with seasonal effects

In order to analyse the effect of seasonal behaviour, the predator-prey model from Section 3.2 was modified as follows:

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{k}\right) - p_x\Phi XY - h_1X$$

$$\frac{dY}{dt} = c\Phi p_x\Phi XY - h_2Y$$

$$\frac{dT}{dt} = -d\Phi T + g_1\Phi U + g_2\Phi V + f\Phi - aXT + (1 - b\Phi)UYp_x\Phi$$

$$\frac{dU}{dt} = aXT - UYp_x\Phi - g_1\Phi U - p_1h_1U$$

$$\frac{dV}{dt} = b\Phi UYp_x\Phi - g_2\Phi V - p_2h_2V$$

where $\Phi = 0.5(\text{sgn}(\sin 2\pi t - 0.5)) + \frac{7}{6}$

The system equations are identical to the model equations in Section 3.2 except that the seasonal parameters are now multiplied by the time-periodic function Φ.

Chapter 4

Solving the system

A mathematical software program, *Maple*, was used to assist in obtaining fixed points and eigenvalues in the following sections.

4.1 Single species model

To review, here is the single-species equation system from section 3.1:

$$\begin{aligned} \dot{X} &= rX\left(1-\frac{X}{k}\right) - h_1 X \\ \dot{T} &= -dT + g_1 U + f - aXT \\ \dot{U} &= aXT - g_1 U - p_1 h_1 U \end{aligned} \tag{4.1}$$

Fixed points are found by setting the time derivatives to zero and solving for

system variables.

4.1.1 Stability analysis

The following two fixed points were obtained for the single-species system:

$$(\overline{X}, \overline{T}, \overline{U}) = \left(0, \frac{f}{d}, 0\right) \tag{4.2}$$

$$(\overline{X}, \overline{T}, \overline{U}) = \left(\frac{k(r-h_1)}{r}, \frac{fr(g_1+p_1h_1)}{\phi}, \frac{fak(r-h_1)}{\phi}\right) \tag{4.3}$$

where $\phi = dr(g_1 + p_1h_1) + p_1h_1ak(r - h_1)$

Fixed point (4.2) represents extinction of the fish population and its associated methyl mercury content. We are interested in analysing the stability of this fixed point to determine all possible conditions that will allow for the population to tend toward extinction. In order to analyse the stability of this fixed point we must look at the sign of the eigenvalues. The following eigenvalues for (4.2) were obtained:

$\lambda_{1,2,3} = r - h_1, -d, -g_1 - p_1h_1$

If all eigenvalues are negative the fixed point is stable, otherwise it is unstable. It is clear from looking at the eigenvalues that λ_2 and λ_3 are negative since all system parameters are positive. λ_1 will be negative (and consequently, fixed point (4.2) stable) if $r - h_1 < 0$. In other words, the population will tend toward extinction if and only if it is overharvested (*i.e.*, $h_1 > r$). If the population is not overharvested, since only one of the three eigenvalues is positive, this fixed point can be classified as a saddle point. When the population is overharvested (*i.e.*, $r - h_1 < 0$), λ_1 is

negative and this fixed point is a stable node. It is unlikely that this fixed point will be reached anytime soon in the study lakes because current harvesting rates are fairly low and population biomass is fairly high so there is no known danger of extinction.

Fixed point (4.3) is biologically meaningful if and only if $r - h_1 > 0$. Thus we only need to discuss the stability of (4.3) under the assumption $r > h_1$.

The eigenvalues for fixed point 4.3 are:

$\lambda_1 = -(r - h_1)$ and $\lambda_{2,3} = -\frac{1}{2r}(\alpha \pm \sqrt{\beta})$, where $\alpha = dr + ak(r - h_1) + g_1 r + p_1 h_1 r$ and $\beta = \alpha^2 - 4dr^2(g_1 + p_1 h_1) - 4akrp_1 h_1(r - h_1)$.

Since we have assumed $r > h_1$, $\lambda_1 < 0$, and hence, the stability of 4.3 is determined by analysis of the remaining eigenvalues. In order to analyse λ_2 and λ_3 we consider α and β. Now, since $r - h_1 > 0$, we obtain $\alpha = dr + ak(r - h_1) + g_1 r + p_1 h_1 r > 0$. If $\beta < 0$ then $\lambda_{2,3} = -\frac{\alpha}{2r} \pm \gamma i$ where γ is a positive, real number. In this case, λ_2 and λ_3 are complex conjugates with negative real parts so fixed point 4.3 is a stable spiral-node.

After performing some algebra (see appendix 6.2.1), it was found that $\beta < 0$ if and only if $\omega^2 < 4g_1 r^2(d - p_1 h_1)$ where $\omega = dr + akr - akh_1 + g_1 r - p_1 h_1 r$.

Further to this, if $p_1 h_1 > d$, $\beta > 0$. It is important to note that, while $p_1 h_1 > d$ guarantees $\beta > 0$, the reverse is not true. That is, if $p_1 h_1 < d$ it is possible that $\beta > 0$ if $\omega^2 > 4g_1 r^2(d - p_1 h_1)$.

If $\beta > 0$, $\lambda_2 < 0$ since $\alpha + \sqrt{\beta} > 0$.

If $\beta > 0$, $\lambda_3 < 0$ if and only if $\alpha - \sqrt{\beta} > 0 \Leftrightarrow \alpha > \sqrt{\beta}$.

$$\alpha > \sqrt{\beta} \Leftrightarrow \alpha > \sqrt{\alpha^2 - 4dr^2(g_1 + p_1 h_1) - 4akrp_1 h_1(r - h_1)}$$
$$\Rightarrow 4dr^2(g_1 + p_1 h_1) + 4akrp_1 h_1(r - h_1) > 0 \tag{4.4}$$

Inequality (4.4) is true (and therefore $\lambda_3 < 0$) when $r - h_1 > 0$. Hence, when $r - h_1 > 0$, fixed point 4.3 is stable since all eigenvalues are negative or complex with negative real parts.

To summarize, the single-species model predicts the existence of two fixed points (4.2 and 4.3). The first fixed point (4.2) is indicative of the situation in which the population has gone extinct and all that is left in the system is methyl mercury contained in the lake water. This fixed point is a stable node when the population is overharvested (*i.e.*, $h_1 > r$) and an unstable saddle point otherwise.

The second fixed point (4.3) is positive and stable when the population is not overharvested (*i.e.*, $r > h_1$) and is negative and unstable otherwise. When stable, it is a spiral-node if $\beta < 0$ and a node otherwise.

When parameter values applicable to the study lakes (listed in Table 3.3) are substituted into the single-species model, the resulting fixed points are:

$$(\overline{X}, \overline{T}, \overline{U}) = (0, 18.3, 0) \tag{4.5}$$

$$(\overline{X}, \overline{T}, \overline{U}) = (14, 4.6, 5.7) \tag{4.6}$$

The corresponding eigenvalues are:

$$\text{Extinction} \qquad \lambda_{1,2,3} = -0.3, -1.1, 1.4 \tag{4.7}$$

$$\text{Viable population} \qquad \lambda_{1,2,3} = -0.6, -2.2, -1.4 \tag{4.8}$$

It is clear upon direct inspection of the fixed points and eigenvalues that fixed point 4.5 is an unstable saddle point, and fixed point 4.6 is a stable node. Hence, it is predicted that the values of the variables will directly approach fixed point 4.6 over time.

4.1.2 Phase portrait analysis

In the previous section it was determined (through eigenvalue analysis) that when parameter values applicable to the Labrador study lakes (see Table 3.3) are substituted in the model, fixed point 4.6 is a stable node. Figure 4.1 shows the location and stability of this fixed point.

The phase portrait consists of two trajectories beginning at different initial conditions. The trajectories flow through phase space and eventually arrive at the stable node. The initial conditions were chosen based on data from the study lakes. The initial conditions used to generate Figure 4.1 are as follows:

$(X_0, T_0, U_0) = (66, 7.4, 23)$

$(X_0, T_0, U_0) = (50, 13, 18)$

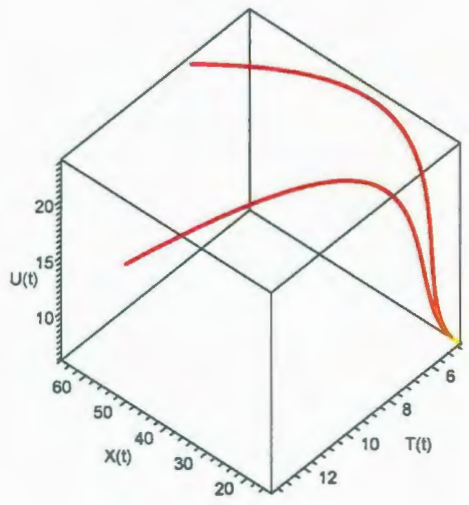


Figure 4.1: Phase portrait for single-species model

4.1.3 Time series analysis

Phase portrait analysis is useful for visualizing the location of the fixed point in phase space but we also want to know how long the system will take to reach the fixed point. To determine this we plot the system variables versus time on a time series graph.

Figure 4.2 is a time series graph of the system variables versus time using the parameter values listed in Table 3.3 and the initial condition $(X_0, T_0, U_0) = (10, 6, 16)$. Population biomass (X) is displayed in red, methyl mercury contained in the lake water (T) is displayed in blue, and methyl mercury contained in the fish population (U) is displayed in green.

The variable trajectories approach equilibrium fairly quickly, within about 7-8 years. Figure 4.2 clearly shows the variables approaching the coexistence fixed point

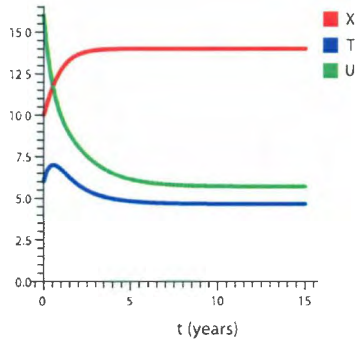


Figure 4.2: Time series plot of X, T and U

(4.6). The population biomass (X) grows immediately and increases until equilibrium is reached. Methyl mercury contained in the lake water (T) increases initially then decreases until reaching equilibrium. Methyl mercury in the population (U) decreases until equilibrium is reached.

The long-term behaviour of the methyl mercury concentration within the population ($\frac{U}{X}$ versus time) is shown in Figure 4.3. This diagram was generated using the initial condition $(X_0, T_0, U_0) = (10, 6, 16)$. The final predicted methyl mercury concentration for the fish population is 0.4 g MeHg·tonne^{-1} fish or 0.4 parts per million (ppm). This is lower than the mercury concentration limit considered by Health Canada to be safe for human consumption. The predicted mercury concentration of 0.4 ppm is lower than field observations for predator fish in Labrador lakes (Anderson *et al.*, 1995; Roux, 2008). This could be due to the model's simplification of methyl mercury intake through the food pathway. All methyl mercury obtained through the

food web is addressed with the parameter a. The predator-prey model discussed in Section 4.2 considers more complicated interactions between methyl mercury and the food web.

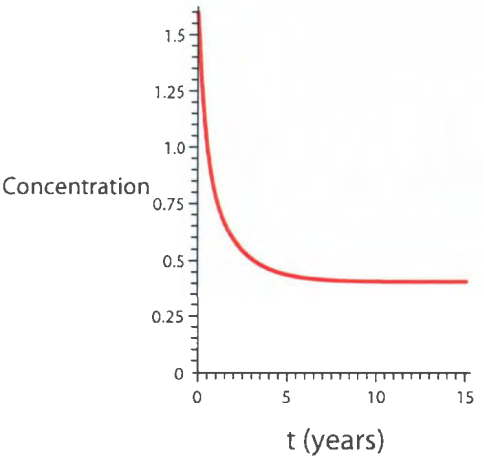


Figure 4.3: Population methyl mercury concentration over time

4.1.4 Numerical sensitivity analysis

In order to determine the parameters for which the model is most sensitive, a numerical sensitivity analysis was performed on each parameter. For each individual parameter, a range of values (within 20% of the value estimated in this study) was assigned and the resulting model behaviour was observed. In particular, fixed point values, eigenvalues, and length of time taken to reach equilibrium were compared using different parameter sets. Numerical ranges tried for each parameter can be found in Table 4.1.

Parameter	Range tested	$\overline{X}$	$\overline{T}$	$\overline{U}$
r	1.6 - 2.4	12.5 - 15	5 - 4.4	5.6 - 5.8
k	16 - 24	10.5 - 17.5	5.7 - 3.9	5.3 - 6
h_1	0.48 - 0.72	15.2 - 12.8	4.7 - 4.7	7.1 - 4.7
d	0.24 - 0.36	14 - 14	5.1 - 4.4	6.2 - 5.4
a	0.08 - 0.12	14 - 14	5.5 - 4	5.4 - 6
g_1	0.34 - 0.5	14 - 14	4.4 - 5.2	5.8 - 5.5
p_1	0.96 - 1.44	14 - 14	5 - 4.4	7 - 4.8
f	4.4 - 6.6	14 - 14	3.7 - 5.6	4.6 - 6.8

Table 4.1: Parameter ranges used for numerical sensitivity analysis and the resulting change to system variables

As expected, $\overline{X}$ was found to be most sensitive to parameters related to population dynamics (r, k, h_1, p_1), and $\overline{T}$ and $\overline{U}$ were most sensitive to parameters related to mercury flux (d, a, g_1, f). None of the parameters had a significant effect on the time taken to reach equilibrium, and there were only slight changes to system behaviour and fixed point magnitude. Methyl mercury concentration was found to be most sensitive to k and p_1 since these parameters had the most effect on $\overline{X}$. The changes to concentration were very small for these parameter ranges however, and methyl mercury concentration did not go above Health Canada's recommended limit of 0.5 ppm.

4.2 Predator-prey model

The predator-prey equation system from section 3.2 is:

$$\dot{X} = rX\left(1 - \frac{X}{k}\right) - p_x XY - h_1 X$$
$$\dot{Y} = cp_x XY - h_2 Y$$

$$\dot{T} = -dT + g_1U + g_2V + f - aXT + (1-b)UYp_x$$

$$\dot{U} = aXT - UYp_x - g_1U - p_1h_1U$$

$$\dot{V} = bUYp_x - g_2V - p_2h_2V$$

Fixed points are found by setting the time derivatives to zero and solving for system variables.

4.2.1 Stability analysis

Three fixed points were obtained for the predator-prey system. The first two fixed points are as follows:

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (0, 0, \frac{f}{d}, 0, 0) \tag{4.9}$$

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (\frac{k(r-h_1)}{r}, 0, \frac{fr(g_1+p_1h_1)}{\phi}, \frac{fak(r-h_1)}{\phi}, 0) \tag{4.10}$$

where $\phi = dr(g_1 + p_1h_1) + p_1h_1ak(r-h_1)$

Fixed point 4.9 represents extinction of both the predator and prey populations and the associated methyl mercury. Fixed point 4.10 represents extinction of the predator population and its associated methyl mercury. The third fixed point represents coexistence of both populations. The coexistence fixed point is very long and cumbersome and, thus, is located in the appendix (6.2.2). There is no known danger of extinction in the study lakes currently because harvesting rates are fairly low and population biomasses are fairly high. However, we are still interested in analysing the stability of fixed points 4.9 and 4.10 to determine all possible conditions that will

cause either or both populations to go extinct.

In order to determine the stability of 4.9 we analyse the eigenvalues. The following eigenvalues were obtained:

$\lambda_{1,2,3,4,5} = r - h_1, -h_2, -d, -g_1 - p_1 h_1, -g_2 - p_2 h_2$

It is obvious that λ_2, λ_3, λ_4, and λ_5 are negative since all system parameters are positive. λ_1 will be negative if and only if $r - h_1 < 0$. This means that if the prey population is overharvested (*i.e.*, $h_1 > r$) fixed point 4.9 will be stable and both populations will approach extinction. Alternatively, if the prey population is not overharvested, fixed point 4.9 will be unstable and the populations will not tend toward extinction.

Fixed point 4.10 represents the situation in which only the predator population tends toward extinction. This fixed point is biologically meaningful if and only if $r - h_1 > 0$. Thus we only need to discuss the stability of 4.10 under the assumption $r > h_1$. The eigenvalues for fixed point 4.10 are:

$\lambda_1 = -r + h_1$

$\lambda_2 = \dfrac{kcp_x(r - h_1) - rh_2}{r}$

$\lambda_3 = -g_2 - p_2 h_2$

$\lambda_{4,5} = \dfrac{1}{2r}(\alpha \pm \sqrt{\beta})$, where $\alpha = -ak(r - h_1) - r(d + g + p_1 h_1)$ and

$\beta = \alpha^2 - 4r^2 d(g_1 + p_1 h_1) - 4akrp_1 h_1(r - h_1)$.

Since we have assumed $r > h_1$, $\lambda_1 < 0$, and hence the stability of 4.10 is determined by analysis of the remaining eigenvalues.

Since $r - h_1 > 0$, $\lambda_2 < 0$ if and only if $kcp_x(r - h_1) < rh_2$.

$\lambda_3 < 0$ since all system parameters are positive.

In order to analyse λ_4 and λ_5, we must consider α and β. Now, since $r - h_1 > 0$, we obtain $\alpha = -ak(r - h_1) - r(d + g + p_1 h_1) < 0$.

System behaviour will change depending if β is negative or positive. It is important to note that β here has the same value as β associated with fixed point 4.3 discussed in section 4.1.1 (single-species model). Therefore, using the same reasoning as was used in section 4.1.1, $\beta < 0$ if and only if $\omega^2 < 4g_1 r^2(d - p_1 h_1)$ where

$\omega = dr + akr - akh_1 + g_1 r - p_1 h_1 r$. Similarly, based on further reasoning from section 4.1.1, the condition $p_1 h_1 > d$ guarantees $\beta > 0$. However, if this condition does not hold it is still possible $\beta > 0$ if $\omega^2 > 4g_1 r^2(d - p_1 h_1)$.

Case 1: $\beta > 0$

If $\beta > 0$, $\lambda_4 = \frac{1}{2r}(\alpha + \sqrt{\beta}) < 0$ if and only if $\alpha + \sqrt{\beta} < 0 \Leftrightarrow \alpha < -\sqrt{\beta}$.

$\alpha < -\sqrt{\beta} \Leftrightarrow \alpha < \sqrt{\alpha^2 - 4dr^2(g_1 + p_1 h_1) - 4akrp_1 h_1(r - h_1)}$

$$\Rightarrow 4dr^2(g_1 + p_1 h_1) + 4akrp_1 h_1(r - h_1) > 0 \ (*)$$

Inequality (*) is true (and therefore $\lambda_4 < 0$) when $r - h_1 > 0$.

The final eigenvalue, $\lambda_5 = \frac{1}{2r}(\alpha - \sqrt{\beta}) < 0$ since $\alpha < 0$ and $\sqrt{\beta} > 0$. Thus, in the case of $\beta > 0$, fixed point 4.10 will be stable if

(i) $r - h_1 > 0$

(ii) $kcp_x(r - h_1) < rh_2$

Case 2: $\beta < 0$

If $\beta < 0$ then $\lambda_{4,5} = \frac{1}{2r}(\alpha \pm \gamma i)$ where γ is a positive real number. In this case, λ_4 and λ_5 are complex conjugates with negative real parts so fixed point 4.10 is a stable

spiral-node.

To summarize the behaviour of fixed point 4.10, when $r - h_1 < 0$ this fixed point is a negative, unstable saddle point. If $r - h_1 > 0$, the fixed point will be stable if and only if $kcp_x(r - h_1) < rh_2$, and will be an unstable saddle point otherwise. Further, when this fixed point is stable it will exhibit spiral behaviour when $\beta < 0$.

The third and final fixed point occurs when both predator and prey populations coexist. In order to determine necessary conditions for a positive coexistence equilibrium, each component of the fixed point was analysed (see appendix 6.2.2 for coexistence fixed point).

(i) $\overline{X} = \dfrac{h_2}{cp_x} > 0$

(ii) $\overline{Y} = \dfrac{kcp_x(r - h_1) - rh_2}{kcp_x^2} > 0$ if and only if $r - h_1 > 0$ and $kcp_x(r - h_1) > rh_2$

(iii) $\overline{T} > 0$ if $r - h_1 > 0$ and $kcp_x(r - h_1) > rh_2$

(iv) $\overline{U} > 0$ if $r - h_1 > 0$ and $kcp_x p_1 h_1 > rh_2$

(v) $\overline{V} > 0$ if $r - h_1 > 0$, $kcp_x p_1 h_1 > rh_2$, and $kcpx(r - h_1) > rh_2$

Hence, it was determined that the coexistence fixed point will be positive when the following conditions are met:

$$r - h_1 > 0 \tag{4.11}$$

$$kcp_x(r - h_1) > rh_2 \tag{4.12}$$

$$kcp_x p_1 h_1 > r h_2 \tag{4.13}$$

The eigenvalues for this fixed point are very long and extremely messy, making it impractical to determine stability analytically. Alternatively, stability analysis was performed numerically by testing ranges of parameter values and observing system behaviour (see Table 4.2 for parameter ranges tested).

When the intrinsic growth rate was set to be greater than the harvesting rate (*i.e.*, $r > h_1$), three of five eigenvalues tested were negative and real for all parameter values tested, while the remaining two eigenvalues were complex with negative real part, indicating that this fixed point is a stable, spiral-node in this case. When the harvesting rate was chosen to be greater than the growth rate (*i.e.*, $h_1 > r$), at least one eigenvalue became positive indicating this fixed point is unstable in this case.

In summary, the predator-prey model predicts the existence of three fixed points, two of which are associated with population extinction (4.9 and 4.10), and one that is associated with population coexistence. The fixed point associated with extinction of both species (4.9) is positive and is stable when the prey population is overharvested (*i.e.*, condition 4.11 not held) and unstable otherwise. The fixed point associated with extinction of only the predator population (4.10) is negative and unstable when the prey are overharvested. When the prey are not overharvested, this fixed point is positive and will be stable if and only if condition 4.12 does not hold. Finally, the coexistence fixed point is positive when conditions 4.11, 4.12, and 4.13 are met, and is negative otherwise. This fixed point is stable when conditions 4.11, 4.12, and 4.13

are met.

When parameter values applicable to Labrador lake systems (listed in Table 3.6) are substituted into the predator-prey model, the resulting fixed points are:

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (0, 0, 18.3, 0, 0) \tag{4.14}$$

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (18.7, 0, 3.9, 7.2, 0) \tag{4.15}$$

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (8, 2.9, 7.4, 3.2, 1.9) \tag{4.16}$$

The corresponding eigenvalues are:

Total extinction $\lambda_{1,2,3,4,5} = -0.3, -1, 1.5, -0.6, -1.1$

Predator extinction $\lambda_{1,2,3,4,5} = -2.6, -0.5, -1.5, -1.1, 0.8$

Coexistence $\lambda_{1,2,3,4,5} = -0.3 + 0.6i, -0.3 - 0.6i, -2.1, -1.5, -0.5$

It is clear upon direct inspection of the fixed points and eigenvalues that fixed points 4.14 and 4.15 are unstable and 4.16 is stable in the case of the study lakes. Therefore, it is predicted that the values of the variables will move away from the total extinction and predator extinction fixed points, and will approach the coexistence fixed point (4.16) over time. Since there is a complex conjugate pair of eigenvalues with respect to the coexistence fixed point, trajectories are predicted to oscillate, spiralling in toward coexistence. Extinction is not currently a threat in Labrador so this behaviour is expected. Fixed points 4.14 and 4.15 are likely stable fixed points

in other lake systems that are subject to mercury contamination and overharvesting of fish populations. The results from this study can be used, with proper buffers, for setting harvesting quotas in such lakes.

4.2.2 Phase portrait analysis

Phase portraits are useful for visualizing locations and stabilities of fixed points. Figure 4.4 shows the location and stability of the coexistence fixed point,

$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = (8, 2.9, 7.4, 3.2, 1.9)$

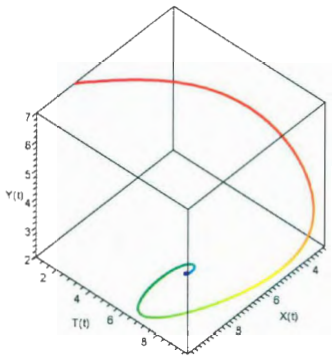
In the previous section it was determined (through eigenvalue analysis) that this fixed point is a stable spiral-node when parameter values applicable to Boreal lake systems are used. The three phase portraits (4.4(a), 4.4(b), and 4.4(c)) show the predator-prey system solution in 3-dimensional space from three different perspectives. The phase portraits consist of one trajectory beginning at the initial condition:

$(X_0, Y_0, T_0, U_0, V_0) = (8, 7, 0.8, 4, 6)$

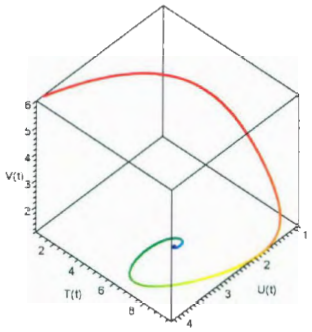
The trajectory spirals through phase space and eventually arrives at the stable spiral-node.

4.2.3 Time series analysis

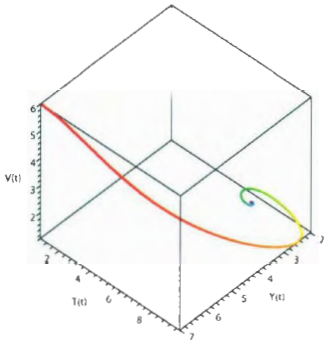
Time series graphs are useful for showing how long a system takes to reach a fixed point. Figure 4.5 is a time series plot of the system variables versus time using the parameter values listed in the Table 3.6 and the initial condition $(X_0, Y_0, T_0, U_0, V_0) = (8, 7, 0.8, 4, 6)$.



(a) X - Y - T space



(b) T - U - V space



(c) Y - T - V space

Figure 4.4: Phase portrait for predator-prey model from three perspectives

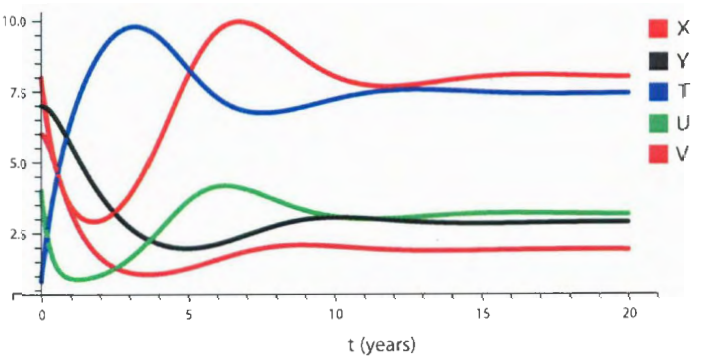


Figure 4.5: Time series plot of system variables. Colours are as follows: X red, Y black, T blue, U green, and V orange.

It takes approximately 15-20 years to reach the coexistence equilibrium. There is some oscillation of the trajectory before the equilibrium is reached. This is expected since it was determined in section 4.2.1 that eigenvalues associated with the coexistence fixed point are complex valued.

The long-term behaviour of the methyl mercury concentration within the populations ($\frac{U}{X}$ versus time and $\frac{V}{Y}$ versus time) is shown in Figure 4.6. This diagram was generated using the initial condition $(X_0, Y_0, T_0, U_0, V_0) = (8, 7, 0.8, 4, 6)$. The final predicted methyl mercury concentration for the prey population is 0.40 g MeHg·tonne^{-1} fish or 0.40 parts per million (ppm), and 0.655 g MeHg·tonne^{-1} fish or 0.655 ppm for the predator population. These values are realistic when compared to measured field data (Anderson *et al.*, 1995; Roux, 2008). The final prey population mercury concentration is below the mercury limit considered safe by Health Canada and the

predator population mercury concentration is above the safe limit, for average size fish. The concentration of methyl mercury is higher in the predator population than in the prey population due to biomagnification.

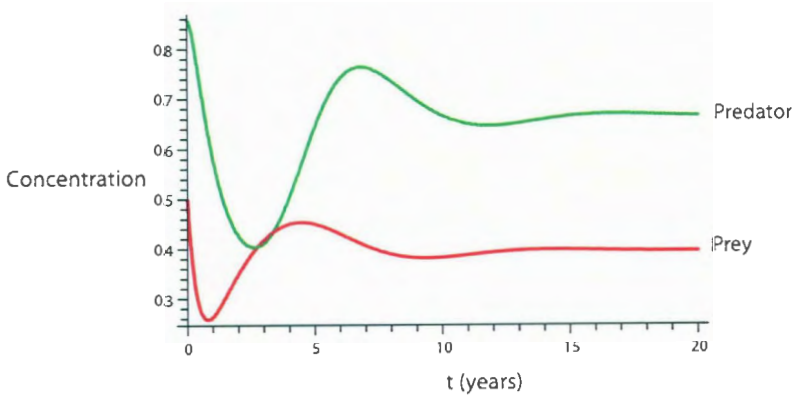


Figure 4.6: Methyl mercury concentration in fish populations over time. Prey methyl mercury shown in orange and predator methyl mercury shown in green.

4.2.4 Numerical sensitivity analysis

A numerical sensitivity analysis was performed on each parameter in order to determine to which parameters the model is most sensitive. For each parameter in the predator-prey model, a range of values (within 20% of the values estimated in this study) was assigned and the resulting fixed points, eigenvalues, and time to reach equilibrium were observed. Numerical ranges tried for each parameter can be found in Table 4.2. The results of the predator-prey model sensitivity analysis were similar

Parameter	Range tested	$\overline{X}$	$\overline{Y}$	$\overline{T}$	$\overline{U}$	$\overline{V}$
r	1.6 - 2.4	6 - 6	1.8 - 3.3	8.7 - 8.8	3 - 2.3	1.5 - 2.1
k	20 - 30	6 - 6	2.3 - 2.8	8.7 - 8.8	2.7 - 2.5	1.7 - 1.9
p_x	0.32 - 0.48	7.5 - 5	2.8 - 2.3	7.7 - 9.6	3 - 2.3	1.9 - 1.7
c	0.2 - 0.3	7.5 - 5	2.3 - 2.8	7.7 - 9.6	3 - 2.3	1.9 - 1.7
h_1	0.4 - 0.6	6 - 6	2.8 - 2.3	9 - 8.5	2.7 - 2.5	2.1 - 1.6
h_2	0.48 - 0.72	4.8 - 7.2	2.8 - 2.3	10 - 7.8	2.2 - 2.9	2 - 1.7
d	0.24 - 0.36	6 - 6	2.6 - 2.6	9.7 - 8	2.8 - 2.4	2.1 - 1.7
a	0.08 - 0.12	6 - 6	2.6 - 2.6	9.8 - 8	2.3 - 2.8	1.6 - 2
g_1	0.34 - 0.5	6 - 6	2.6 - 2.6	8.6 - 8.9	2.6 - 2.5	1.9 - 1.9
g_2	0.34 - 0.5	6 - 6	2.6 - 2.6	8.6 - 8.9	2.5 - 2.6	1.9 - 1.8
p_1	0.96 - 1.44	6 - 6	2.6 - 2.6	9 - 8.6	2.1 - 2.4	2 - 1.7
p_2	0.96 - 1.44	6 - 6	2.6 - 2.6	8.9 - 8.6	2.6 - 2.5	2.2 - 1.6
b	0.64 - 0.96	6 - 6	2.6 - 2.6	9.2 - 8.4	2.7 - 2.5	1.5 - 2.1
f	4.4 - 6.6	6 - 6	2.6 - 2.6	7 - 10.5	2.1 - 3.1	1.5 - 2.2

Table 4.2: Parameter ranges used for numerical sensitivity analysis and the resulting change to system variables

to the results of the single-species model sensitivity analysis in that the population variables ($\overline{X}$ and $\overline{Y}$) were most sensitive to the parameters related to population dynamics (r, k, h_1, h_2, p_1, p_2, c, p_x), and the methyl mercury-related variables ($\overline{T}$, $\overline{U}$ and $\overline{V}$) were most sensitive to parameters related to methyl mercury flux (f, d, a, b, g_1, g_2). It is interesting that $\overline{U}$ and $\overline{V}$ are not affected very much by parameters related to population dynamics, particularly in terms of harvesting as a strategy to reduce mercury contamination in fish. The results here suggest that harvesting would not be an effective strategy which is in accordance with Surette, Lucotte & Tremblay's (2005) empirical studies in northern Quebec.

In terms of fixed point magnitude, changes to most parameters produced expected slight changes to system variables. The most significant change to the variables related

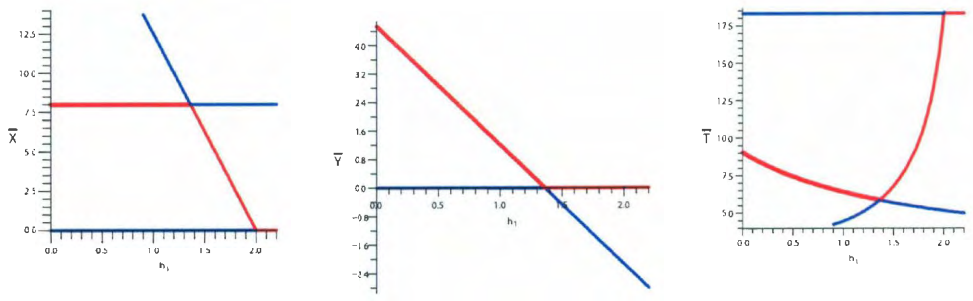
to population biology ($\overline{X}$ and $\overline{Y}$) occurred when the population growth rate (r) was varied. However, even in this case overall system behaviour remained the same. The most significant changes to methyl mercury-related system variables were caused by changing methyl mercury input to the lake system (f). As f increased, $\overline{T}$, $\overline{U}$ and $\overline{V}$ increased in direct proportion to f. This is an unusual result since the system is clearly nonlinear.

Methyl mercury concentration in the prey population did not change very much throughout the sensitivity analysis. The predator population concentration was sensitive to the rate of methyl mercury input (f) with concentrations ranging from 0.5-0.84. This is fairly significant because at the lowest input rate ($f = 4.4$) the concentration is within Health Canada's threshold for safe consumption but at the higher input rate ($f = 6.6$) methyl mercury concentration exceeds the limit.

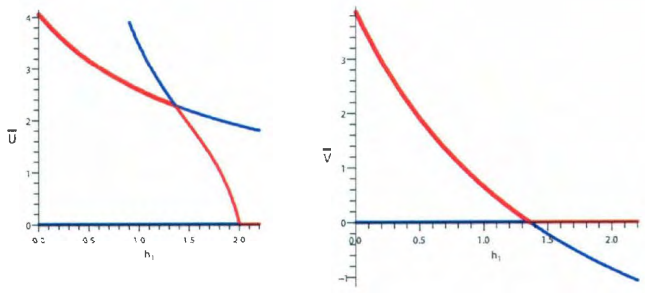
The most notable effect on time taken to reach equilibrium occurred when a change was made to the predator functional response (p_x). As p_x increases, the system takes longer to reach equilibrium.

4.2.5 Bifurcation analysis - varying h_1

In order to determine the effects of prey harvesting, we vary the value of h_1 and examine the resulting changes in fixed points. Figure 4.7 shows how the $\overline{X}, \overline{Y}, \overline{T}, \overline{U}$ and $\overline{V}$ coordinates of the fixed point change as the parameter h_1 is varied. These diagrams also show ranges of h_1 for which each fixed point is stable (denoted by red line). It is clear from the bifurcation diagram that transcritical bifurcations occur at $h_1 = 1.36$ and at $h_1 = 2$.



(a) h_1 varied with respect to $\overline{X}$ (b) h_1 varied with respect to $\overline{Y}$ (c) h_1 varied with respect to $\overline{T}$



(d) h_1 varied with respect to $\overline{U}$ (e) h_1 varied with respect to $\overline{V}$

Figure 4.7: Bifurcation diagrams (h_1 varied)

At both bifurcation points the system is undergoing an exchange of stability. When h_1 is low ($h_1 < 1.36$), the coexistence fixed point is stable. During this time the prey harvesting rate is low enough that both predator and prey fish populations survive in the lake system. As h_1 increases past $h_1 \geq 1.36$, system stability shifts to fixed point 4.10 and $\overline{Y} = \overline{V} = 0$. At this point, harvesting of the prey has increased to the extent that the predator population has become extinct due to increased competition for food, and any methyl mercury associated with the predator population has left the system. As h_1 increases further, the prey population biomass quickly decreases which causes $\overline{U}$ to decrease. Finally, when $h_1 \geq 2$, the extinction fixed point (4.9) gains stability. At this point both prey and predator populations are extinct and the only mercury in the lake system is contained in the lake water (Figure 4.7(c)).

It is important to note that the bifurcation diagrams verify results of the stability analysis. The stability analysis (see section 4.2.1) showed that fixed point 4.14 is stable if and only if $h_1 > r$. The bifurcation diagrams clearly show that when $h_1 > r$ (where $r = 2$ in this case) both predator and prey populations are extinct and fixed point 4.14 is stable. Further, the stability analysis showed that fixed point 4.15 is stable if and only if $kcp_x(r-h_1) < rh_2$. This condition is satisfied only when $h_1 > 1.36$. The bifurcation diagrams clearly show that when $h_1 > 1.36$ the predator population is extinct and fixed point 4.15 is stable.

In summary, the bifurcation diagrams show that the coexistence fixed point will be stable until the prey harvesting rate increases past a certain threshold ($h_1 = 1.36$ in this case) at which point the predator population will become extinct. Further, if the harvesting rate increases past a second threshold ($h_1 = 2$ in this case) the prey

population will also become extinct.

While the bifurcation analysis using h_1 does not pertain directly to methyl mercury behaviour within the system, it is interesting from a population biology perspective. The bifurcation diagrams show clearly at what harvesting rates the populations become in danger of extinction. Harvesting rates are relatively low in the Labrador study lakes, however, this information could be used (with careful buffering) to set harvesting rates in other lakes.

4.3 Comparison of the models

The system equations of the single-species and predator-prey models look quite different. However, most of the principles used for model construction are the same. The difference between these models is that the predator-prey model includes a second population and the associated mercury flux interactions. This small (but important) difference in the model changes some of the long-term system behaviour.

In terms of stability, the predator-prey model has one more fixed point than the single-species model. Fixed points in both models are very similar in that each model has one fixed point representing population survival, and one fixed point representing population extinction. The single-species system has only one fixed point representing survival of the population whereas the predator-prey model has two, one fixed point representing both predator and prey population survival, and one fixed point representing survival of only the prey population. When parameter values applicable to the study lakes are used, extinction fixed points are unstable in both models and

population existence fixed points are stable.

Both models require the condition $r - h_1 > 0$ in order to maintain system stability. If this condition is not held, the extinction fixed point becomes stable. In the predator-prey model there are additional conditions required to ensure the coexistence fixed point remains stable (refer to section 4.2.1).

Phase portraits generated using parameter values relevant to the study lakes show stable system behaviour long-term in both models. The survival fixed point is a stable node in the single-species system and, thus, this fixed point is approached directly. The coexistence fixed point is a stable spiral point in the predator-prey model, and so this system exhibits periodic behaviour as the fixed point is approached.

In terms of time taken to reach equilibrium, the single-species system approaches its fixed point much faster than the predator-prey system, 7-8 years versus 15-20 years. It is no surprise that the single-species system achieves equilibrium faster since it is a node rather than a spiral point.

4.4 Seasonal effect on models

The following subsections contain mathematical analyses of the seasonal models described in sections 3.3.1 and 3.3.2.

4.4.1 Single-species model with seasonal effects

Phase portrait analysis

Figure 4.8 is a phase portrait of the single-species system with seasonal effects. The phase portrait consists of one trajectory beginning at an initial condition $(X_0, T_0, U_0) = 13, 3, 3)$. The phase portrait shows that after some initial fluctuation the trajectory begins to follow a periodic orbit, or a limit cycle. The model predicts that when winter temperatures and spring snowmelt are considered, the system will never reach a fixed point but, rather, will exhibit cyclical behaviour around the fixed point.

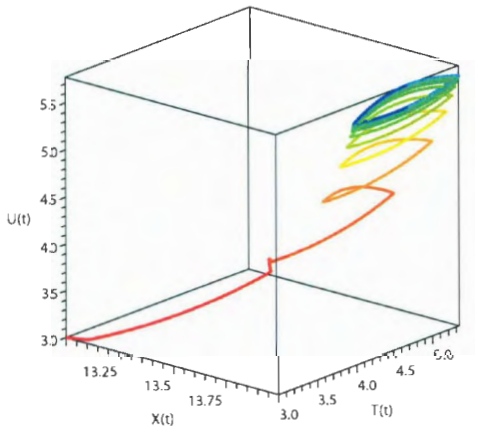


Figure 4.8: Phase portrait of single-species model with seasonal effects

Time series analysis

The time series graph shown in Figure 4.9 was generated using parameter values listed in Table 3.3 and the initial condition $(X_0, T_0, U_0) = (13, 3, 3)$. This diagram shows that the methyl mercury-related variables T and U exhibit periodic behaviour long-term (shown in blue and green respectively) but the fish biomass (X, shown in red) does not. This result is expected since the model was constructed with the assumption that methyl mercury does not affect population growth rate, and the biological parameters affected by seasonality are predator-prey parameters (b, c, p_x) which are not included in this model.

The time series graph shows significantly more variation in T than in U. Throughout the limit cycle the value of T fluctuates by approximately 1.5 g·yr^{-1} compared with 0.4 g·yr^{-1} for U. The value of both variables fluctuates around the fixed point identified in the single-species model without seasonal effects. In this model, T fluctuates between approximately 4-5.4 g compared with 4.6 g in the single-species system (see Section 3.1), and U fluctuates between 5.5-5.9 g compared with 5.7 g.

The methyl mercury concentration predicted in this model ranges from 0.39-0.42 ppm throughout the cycle. This concentration corresponds to the methyl mercury concentration of 0.4 ppm predicted by the single-species model without seasonal effects. Once again, this concentration is somewhat lower than field measurements (Anderson *et al.*, 1995; Roux, 2008). One reason for this could be the lack of system interactions in the single-species model. The missing predator-prey interactions may cause the results to be less reliable. The discrepancy could also be a result of the

generality of the seasonal function. Applying the same seasonal square wave function to all seasonal parameters is probably not an accurate portrayal of the system behaviour. Changing the model in this manner can provide a general idea as to qualitative changes to the system behaviour caused by seasons, however it is unlikely to provide accurate quantitative results.

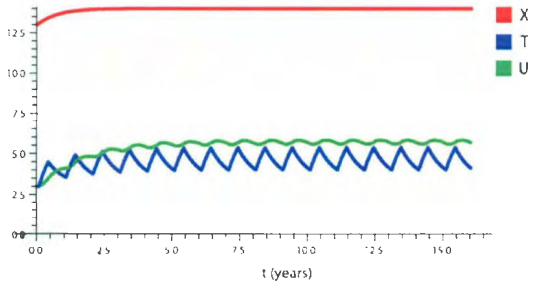


Figure 4.9: Time series plot of single-species model variables (with seasonal effects).

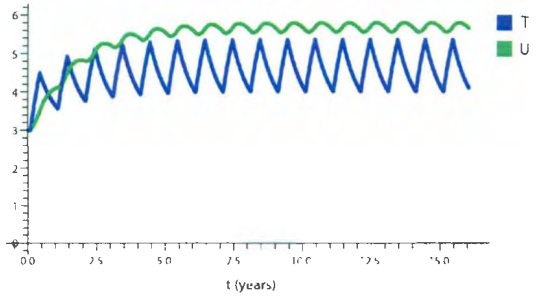


Figure 4.10: Detail of time series plot of seasonal single-species model variables.

4.4.2 Predator-prey model with seasonal effects

Phase portrait analysis

Figure 4.11 is a phase portrait of the predator-prey system with seasonal effects. This phase portrait consists of one trajectory beginning at an initial condition. It is clear from the phase portrait that the model exhibits cyclical behaviour when the seasonal effects of cold winter temperatures and spring snowmelt are introduced, eventually approaching a limit cycle. The initial condition used to generate the phase portrait is:

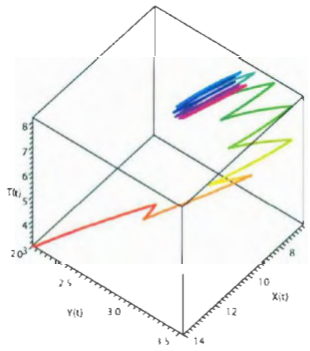
$$(X_0, Y_0, T_0, U_0, V_0) = (14, 2, 3, 2.5, 1)$$

Time series analysis

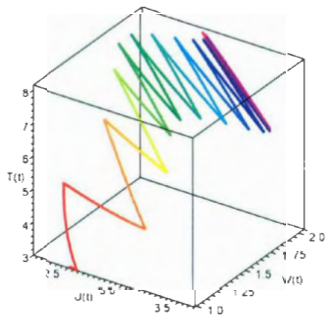
Figure 4.12 shows a time series graph for the predator-prey model with seasonal effects. The graph was generated using the parameter values in Table 3.6 and the initial condition $(X_0, Y_0, T_0, U_0, V_0) = (14, 2, 3, 2.5, 1)$. From this diagram we can see that all variables exhibit long-term periodic behaviour when seasonal effects are introduced.

Figure 4.12 shows that the limit cycle behaviour will be achieved within approximately 15 years. The variables range around the fixed point identified in the predator-prey model without seasonal effects. The range of variable magnitude throughout the cycle is fairly small.

Furthermore, methyl mercury concentrations within the fish populations are almost identical to the concentrations in the predator-prey model without seasonal



(a) X - Y - T space



(b) T - U - V space

Figure 4.11: Phase portrait of predator-prey model with seasonal effects

effects. For the prey population, concentration ranges from approximately 0.36-0.41 ppm in this model compared to 0.4 ppm in the predator-prey model in Section 3.2, and the predator population concentration is 0.65 ppm at both the cycle high and low compared to 0.655 ppm in the predator-prey model without seasonal effects.

It is interesting to note that the methyl mercury concentration within each fish population does not change much between the cycle high and low points. This is a realistic result when compared with measured field data since field data does not

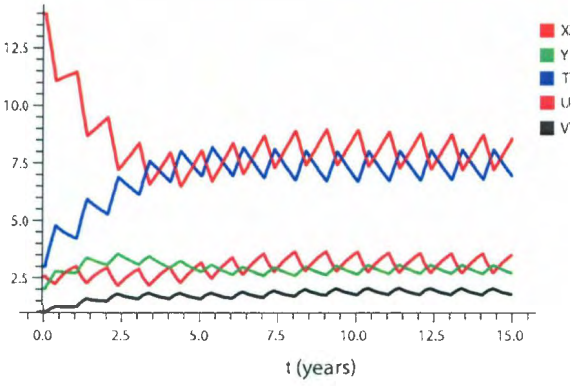


Figure 4.12: Time series plot of predator-prey model variables with seasonal effects.

show a significant difference in methyl mercury concentration at different times of the year.

Variable	Seasonal model cycle high	Seasonal model cycle low	No seasonal effect (fixed point value)
X (tonnes·km^{-2})	8.7	7.2	8
Y (tonnes·km^{-2})	3.1	2.6	2.9
T (g·km^{-2})	8.2	6.8	7.4
U (g·km^{-2})	3.6	2.6	3.2
V (g·km^{-2})	2.0	1.7	1.9

Table 4.3: Comparison of variable magnitude between predator-prey model with seasonal effects (Section 4.4.2) and predator-prey model without seasonal effects (Section 3.2)

Chapter 5

Discussion

Two dynamical systems models were developed and analysed in this study. The first model considered methyl mercury dynamics between a lake environment and a single fish population, while the second model incorporated a predator-prey relationship between two fish species, and the associated methyl mercury behaviour.

The development and analysis of the models described here are quite different than those of previous methyl mercury models. The majority of methyl mercury models to date have been statistical models or mass-balance models that do not use dynamical systems methods of analysis. Prior to this, the only dynamical systems models developed for contamination of aquatic systems dealt with toxicants that kill fish populations.

The predator-prey models developed here predict system behaviour more accurately than the single-species models when model results are compared with field data. This was expected since the predator-prey models contain more system interactions

thus, better reflecting the actual behaviour in the environment. For this reason, the remainder of this discussion is focused on the predator-prey models.

Overall, the predator-prey model predicts the lake system will reach equilibrium in about 15-20 years if conditions remain the same. When the system is at equilibrium, mercury levels in prey fish will be safe for human consumption (0.4 ppm) however, mercury content in predator fish will exceed consumption guidelines for fish that are average size and above (0.655 ppm). This means that, if environmental conditions remain the same, fish in top trophic levels should be consumed with caution. Consumption may need to be limited such that top predator fish are eaten less often, or not at all. This may be a concern for the Innu in particular since fish are a significant part of their diet. Many fish may still be eaten with no problem but intake of top predator fish may need to be monitored. That being said, it is important to bear in mind that the model predictions are very general and that some lakes, even some specific areas within lakes, have different fish mercury concentrations than others. This means that fish obtained from certain areas may be safer than others. The model results should be used in conjunction with field data when making recommendations to fish consumers.

When seasonal effects on system parameters are incorporated into the model, the system exhibits cyclical behaviour rather than approaching a fixed point. The seasonal model predicts the system will attain limit cycle behaviour within 15 years. This model predicts final mercury concentrations very similar to that of the predator-prey model without seasonal effects included. While this model provides a general idea as to qualitative changes to system behaviour caused by seasonal effects, more

work needs to be performed on the seasonal function applied to each parameter in order to obtain accurate quantitative results.

If atmospheric mercury emissions were to decrease there would almost certainly be a related change to methyl mercury within the lake system. It is difficult to analyse changes to atmospheric mercury emissions directly using the model described here because the model considers methyl mercury input to the lake and atmospheric emissions consist primarily of Hg^0 and $Hg[II]$. The relationship between the amount of Hg^0 and $Hg[II]$ deposited in a lake and the subsequent methyl mercury produced is not simple and is poorly understood. However, the model described here can provide information regarding changes to system behaviour that result from a change to methyl mercury input. The model shows that fish methyl mercury concentrations are positively correlated with methyl mercury input. More specifically, methyl mercury input must decrease by 25% in order for predator fish to have methyl mercury concentrations at 0.5 ppm or lower (Health Canada guideline for safe human consumption). Furthermore, if methyl mercury input increases by 35%, prey fish methyl mercury concentrations will exceed the guideline.

The models described here were developed with the Labrador study lakes in mind, however, these models can be applied to other lake environments fairly easily. The model equations can remain the same for any lake that has been subjected to mercury contamination, however, parameter values may need to change. Further, if the lake being studied is not subjected to harvesting, natural death rates should be substituted for harvesting rates.

In addition to lake systems, the models described here can be applied to reservoir

systems with minor adjustments. To model a reservoir system, a change to the methyl mercury input term in the lake mercury equation ($\dot{T}$) is required such that, in addition to the constant methyl mercury input (f), there is a large initial methyl mercury input. This large input represents methyl mercury that is released from soil when the reservoir is initially flooded. Once this change has been made to the model, the same analysis techniques can be used for the reservoir system. Field data has shown that the time required for fish methyl mercury levels to return to background levels in northern Boreal reservoirs is actually quite close to the return time predicted by the model in the study. Return times have been observed to be approximately 25 years in Labrador reservoir systems (Anderson *et al.*, 1995) compared with a return time of approximately 15 - 20 years predicted by this model. If the model were adjusted to include a large initial methyl mercury input the return times predicted by the model would likely match field observations even more closely.

While the models developed here are valid and robust, there are several ways they can be improved. Further research in both mercury flux and population behaviour in lake systems could improve model accuracy.

First of all, more accurate parameter estimations will improve the accuracy of the model predictions. In particular, the value of parameters related to population dynamics (e.g. r, k, p_x, c) were difficult to estimate from literature data. Sensitivity analysis showed that the predator-prey model is most sensitive to the predator functional response (p_x) so this parameter is a good candidate for further research.

Secondly, both models in this study assume that methylation and methyl mercury accumulation rates are the same throughout the entire lake. However, some field

studies in Labrador have shown that these rates are different in pelagic zones than in littoral zones. It would be very interesting (and practical) to incorporate this into the model. This would certainly increase the accuracy of the model, although it is uncertain what (if any) change to the model results would occur.

Finally, the models developed here ignore a time delay that occurs from the point that mercury is excreted from fish as inorganic mercury and the time it is again available for uptake as methyl mercury. Incorporating this time delay would certainly improve model accuracy, however, it would complicate the model equations and more complex mathematical analysis techniques would be required.

Future work could also include Poincaré map analysis of the models. This type of analysis can be used to further study the system's approach to equilibrium or the transition to limit cycle behaviour in the case of the seasonal system.

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Chapter 6

Appendix

6.1 Parameter calculations

6.1.1 Estimation of g_1 and g_2

The methyl mercury removal process within fish exhibits exponential decay behaviour. The methyl mercury half-life is the amount of time taken for half the total methyl mercury contained within a fish to be removed. Calculations for estimated value of g_1 and g_2 are as follows:

$M(t) = M_0 e^{-\lambda t}$ (*)

where $M(t)$ is the amount of methyl mercury observed in the population at time t, $M_0 = M(0) =$ the initial amount of methyl mercury, and λ is the rate of decay per unit time.

It follows that the methyl mercury half-life can be defined in the following way.

For the decaying methyl mercury, we know that

$\frac{M(t)}{M_0} = \frac{1}{2}$ where t = half-life of methyl mercury = 600 days (Miettinen *et al.*, 1969).

By substituting into equation (*) we get

$\frac{M(t)}{M_0} = \frac{1}{2} = e^{-\lambda t}$

$\ln(\frac{1}{2}) = \ln e^{-\lambda t}$

$\ln(\frac{1}{2}) = -\lambda t$

$\lambda = \frac{0.6931}{600}$ days = 0.00115/day

0.00115/day * 365.25 days/year = 0.42/year

0.42/year is the estimated value used for g_1 and g_2

6.1.2 Estimation of d

The value of total methyl mercury removed from the lake (d) was calculated to be the sum of methyl mercury removed due to sediment burial (d_1), demethylation in the water column (d_2), and tributary outflow (d_3).

$d = d_1 + d_2 + d_3$

Sediment burial (d_1)

Watras *et al.* (1994) found that methyl mercury was buried at a rate of 91 ng·m^{-2}·yr^{-1} in the sediment of Little Rock Lake, Wisconsin. Using this rate, methyl mercury lost through sediment burial in the study lakes is:

No Name: 27.43 x 10^{6}m^2 * 91 ng·m^{-2}·yr^{-1} = 2.5 g·yr^{-1} out of 7.4 g total $\Rightarrow$ d_2 = 0.3yr^{-1}

Panch: 20.65 x 10^{6}m^2 * 91 ng·m^{-2}·yr^{-1} = 1.9 g·yr^{-1} out of 13.5 g total $\Rightarrow$ d_2 =

0.14yr^{-1}

Rocky Pond: 6.21 x 10^6m^2 * 91 $\text{ng}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ = 0.5 $\text{g}\cdot\text{yr}^{-1}$ out of 0.8 g total $\Rightarrow d_2 = 0.6\text{yr}^{-1}$

Shipiskan: 17.21 x 10^6m^2 * 91 $\text{ng}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ = 1.5 $\text{g}\cdot\text{yr}^{-1}$ out of 55 g total $\Rightarrow d_2 = 0.02\text{yr}^{-1}$

The mean of these four values is $d_1 = 0.27\text{yr}^{-1}$

Demethylation in the water column (d_2)

Demethylation in the water column occurs at such a low rate that it was omitted in the calculation of d (*i.e.*, $d_2 = 0$).

Tributary removal (d_3)

There was no suitable data available on rates of methyl mercury removal from tributaries and is assumed to be small in our lakes. The rate d_3 was assumed to be negligible in this analysis.

Thus, the value of d was calculated to be:

$d = 0.27\text{yr}^{-1} + 0 + 0 \approx 0.3\text{yr}^{-1}$

6.2 Stability analysis

6.2.1 Conditions required for $\beta < 0$

As stated in section 4.1.1, $\beta = \alpha^2 - 4dr^2(g_1 + p_1h_1) - 4akrp_1h_1(r - h_1)$ where $\alpha = dr + ak(r - h_1) + g_1r + p_1h_1r$.

A second way to express β is $\beta = \omega^2 - 4g_1r^2(d - p_1h_1)$ where $\omega = dr + akr - akh_1 + g_1r - p_1h_1r$

$$\beta < 0 \Leftrightarrow \omega^2 - 4g_1r^2(d - p_1h_1) < 0$$
$$\Rightarrow \omega^2 < 4g_1r^2(d - p_1h_1)$$

Thus, we have shown that $\beta < 0$ if and only if $\omega^2 < 4g_1r^2(d-p_1h_1)$. Further to this, if $p_1h_1 > d$, than $4g_1r^2(d - p_1h_1) < 0$ and $\beta > 0$. While $p_1h_1 > d$ guarantees $\beta > 0$, the reverse is not true. If $p_1h_1 < d$ it is possible that $\beta > 0$ if $\omega^2 > 4g_1r^2(d - p_1h_1)$.

6.2.2 Coexistence fixed point for predator-prey model

The coexistence fixed point for the predator-prey model is as follows:

$$(\overline{X}, \overline{Y}, \overline{T}, \overline{U}, \overline{V}) = \left(\frac{h^2}{cp_x}, \frac{kcp_x(r - h_1) - rh_2}{kcp_x^2}, \right.$$
$$\frac{fcp_x(kcp_x(r - h_1 + g_1 + p_1h_1) - rh_2)(g_2 + p_2h_2)}{\gamma},$$
$$\left. \frac{ah_2fkcp_x(g_2 + p_2h_2)}{\gamma}, \frac{fh_2ab(rh_2 - kcp_x(r - h_1)}{\gamma} \right)$$

where $\gamma = ah_2^2p_2bkcp_x(r - h_1) + g_2dkc^2p_x^2(r - h_1) + p_2h_2dkc^2p_x^2(r - h_1) + g_2dcp_x(kcp_xp_1h_1 - rh_2) + p_2h_2dcp_x(kcp_xp_1h_1 - rh_2) + p_2h_2^2a(p_1h_1kcp_x - rh_2b) + kc^2p_x^2g_1d(g_2 + p_2h_2) + g_2ah_2p_1h_1kcp_x$.