

**The Development and Application of a Computer Simulation Model
for Evaluating and Predicting the Effects of Reservoir Development and
Hydro Operations on four fish species in Manitoba, Canada**

**by
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**A Thesis Submitted in Partial Fulfilment of the Requirements for the Degree Master
of Natural Resources Management**

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HYDRO OPERATIONS ON FOUR FISH SPECIES IN MANITOBA, CANADA**

BY

CAMERON C. BARTH

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree**

of

MASTER OF NATURAL RESOURCE MANAGEMENT

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ABSTRACT

Numerous river systems in Manitoba, Canada, and around the world have been affected by the environmental changes that follow hydroelectric development and associated hydro operations. Predicting the potential impacts of a proposed or existing hydroelectric development on fisheries resources is a complex process. Persons evaluating the impacts may be faced with the necessity of making decisions even though all of the necessary or desirable information is not available. The tool developed in this research incorporates physical and biological information and is offered as an aid towards making the “best” decision possible, consistent with the level of knowledge and time available.

A computerized simulation model that can be used to simulate the effects of reservoir development and hydro operations on four fish species common to hydroelectric reservoirs in Manitoba was developed in this research. The model framework incorporated four levels. Physical features of the reservoir (level 1), abiotic features of the reservoir (level 2), biotic features of the reservoir (level 3) and fish (level 4). Four species of fish were included in the model: northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), longnose sucker (*Catostomus catostomus*) and walleye (*Stizostedion vitreum*). Since reservoir operations may affect each fish species differently, depending upon age of the fish, seven life-cycle phases comprised level 4 of the model, ranging from the egg life phase to the mature adult life phase.

In total, the results of twelve (model simulations) alternative hydroelectric discharge scenarios were discussed in this research. Results suggested that an operating strategy which minimized water level fluctuations would benefit reservoir fish populations.

However, biological systems are complex, and the search for a precise answer through the use of models given existing knowledge and understanding of reservoir systems is an unrealistic objective to achieve. This model should be used to provide decision makers with a tool to help assess the general trend and magnitude of change in fish populations that results from hydroelectric development and associated hydro-operations.

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Chapter 1: Introduction

1.0 Background

The province of Manitoba has been referred to as the “Hydro Province” due to the large amount of hydroelectric potential that exists within its boundaries. Currently, 14 hydroelectric generating stations, providing approximately 5000 MegaWatts (MW) of power operate in Manitoba and others are planned for the immediate future (Manitoba Hydro 1995).

Numerous river systems in Manitoba, and around the world have been affected by reservoir development and the hydro operations that follow. Although the biological impacts resulting from reservoir development and hydro operations have been extensively studied, predicting potential impacts is difficult and deserves continued attention.

Canadian legislation requires developers to determine the environmental changes that result from the construction and operation of large-scale developments. Regulators require that environmental impact assessments are completed prior to project development to ensure that the biological impacts associated with the development are considered (Sadar 1994). This requirement, and the potential for further hydroelectric development in Manitoba and throughout Canada, has created demand for an efficient tool to further understand, evaluate and predict environmental impacts resulting from reservoir development and hydro operations (Therien 1981).

Reservoir development is usually accompanied by environmental changes (Rosenberg et al. 1987). Hydroelectric impoundments essentially create lacustrine (lake type) conditions from the existing riverine (river type) conditions. The alterations of river

flows and water levels result in changes to water quality, water temperature and turbidity, which affect many biological aspects of the aquatic ecosystem (Bietz 1988, Rosenberg et al. 1995). Over time, the entire biological community must adapt to the new conditions created by the reservoir. Shifts in species abundance, distribution, and diversity of plant, animal, insect and fish may be observed (Fowler 1972; Therien 1981; Baker and Davies 1991).

The impact that reservoir development and hydro operations have on fish is a very important issue. Fish are not only an important source of sustenance and income for commercial and domestic fishermen, but are also important to the culture of many native people. Changes to the abundance and composition of fish communities following hydroelectric developments often are not immediate, and may occur over many years as the biological community adapts to the new conditions created by the reservoir and the operations associated with the reservoir.

Fisheries management is the practice of analyzing and implementing decisions to maintain or alter the structure, dynamics and interactions of habitat and aquatic biota to achieve specified human goals and objectives through the aquatic resource (Lackey 1978). Fisheries managers predict the consequences of a proposed fisheries management decision in a number of ways including: rules of thumb, past experience, formal models, experimentation, trial and error, and “educated guesses”. Development of a method or tool that could be used by engineers, biologists, fisheries managers and hydro developers to predict and investigate the long-term impacts that hydro development and hydro operations have on the fish populations would be an extremely useful and valuable application.

Models have long been used by fisheries managers to describe fish populations. The objective of most fisheries models is to calculate optimal yields for commercial fish species (Schaefer 1954, Beverton Holt 1957, Ricker 1975). These models often focus on analyzing the population structure of fisheries systems and/or analyzing how the population structure of a fish species may change in response to commercial fish harvest. The most frequent application of fisheries models has been to marine commercial fisheries, while relatively few models have been applied to inland fisheries. Historically, models have not been developed to describe the impact that reservoir development and subsequent hydroelectric operations have on fisheries resources.

Computer simulation and optimization modeling tools are currently used by hydro utilities to plan hydro-power production and to make operational decisions (Simonovic and Burn 1989; Alberto et al. 1990, among many). Hydro-power scheduling models have been developed to help reservoir operators optimize reservoir use and resolve conflicts among competing users. Unfortunately, current scheduling models rarely address fishery concerns because models suitable for predicting the impacts changing environment conditions of fish populations are scarce (Plosky 1986).

Modeling can be an extremely useful tool for impact analysis. System analysis through computer simulations is being used increasingly by biologists to further the understanding of complex ecological systems that change over time (Hannon and Ruth 1997). Rather than replacing detailed biological studies, computer simulation modeling is a complementary activity, providing a method for integrating information on a number of important variables. The main goal of computer simulation models is to aid in hypothesis formulation and testing, and to use the models to compare the outcomes of

alternative management decisions. Development and application of a computer simulation model to aquatic ecosystems affected by hydroelectric development would provide a further understanding of the system, provide a tool to aid in making predictions and allow alternatives management scenarios to be compared. Computer simulation modeling and system analysis provide a unique opportunity to develop a thorough understanding of northern Canadian reservoirs (Therien 1981).

This research focused on the development of a computerized simulation model that can be used to simulate the effects that reservoir development and hydro operations have on four fish species common to hydroelectric reservoirs in Manitoba. The model used techniques from previous models, plus several new techniques and ideas. This exercise was an attempt at bridging a gap between available fisheries models and modeling techniques, and the information needs (important considerations) of engineers, biologists, and developers, that should be considered when predicting the impacts of hydroelectric developments and associated operations on reservoir ecosystems.

1.1 Issue statement

One of the most challenging tasks facing hydroelectric developers and scientists is predicting how fish populations react to environmental changes induced by reservoir development and reservoir operations. After 50 or more years of studying hydroelectric reservoirs, biologists have accumulated many observations on the biological changes resulting from their development. Although many of these observations may be contradictory, enough research is available to develop conceptual models of how hydroelectric development affects fisheries (Plosky 1986).

Does our knowledge of the impacts of reservoir development allow for biologists to predict changes in fish abundance in an aging reservoir? In the context of hydroelectric development, can developments be designed or managed to reduce potential adverse impacts on fish? Can we make predictions concerning what type of operational strategy (water release) may benefit fisheries in aging impoundments (Kimmel and Groeger 1986)?

This research attempts to answer the above questions through the development of a computer simulation model. The model was based on scientific literature, physical reservoir data and fisheries survey data collected from the Limestone reservoir on the Nelson River. Fish species included in the model were northern pike (*Esox lucius*), longnose sucker (*Catostomus catostomus*), lake whitefish (*Coregonus clupeaformis*) and walleye (*Stizostedion vitreum*). The purpose was to design a model with the ability to test the impact of alternative reservoir operations strategies on these four fish species in a hydroelectric reservoir, and in the process of developing and testing the model, further our understanding of the changes associated with reservoir development and hydro operations.

1.2 Objectives

The main objectives of the research were:

- 1) to further understanding of the impact that reservoir development has upon the aquatic reservoir environment;
- 2) to improve the ability to predict the impacts of reservoir development and hydro operations on populations of fish;
- 3) to develop a model framework with the following characteristics and abilities:

- a) to enable the discussion of results among engineers, biologists and other stakeholder groups;
 - b) to provide the capability to easily manipulate model inputs to test new hypotheses, predictions, and ideas;
 - c) to develop a model framework which is flexible (i.e., easily added to), and capable of being applied to a future hydroelectric developments; and,
 - d) to be capable of being used to predict trends in fish abundance following reservoir development.
- 4) to use the model to investigate the impact that alternative reservoir operations strategies may have on populations of northern pike, lake whitefish, longnose sucker and walleye;
 - 5) to identify where deficiencies in knowledge of the reservoir ecosystem exist;
 - 6) to identify where further research and data collection in the Limestone reservoir is needed.

1.3 Methods

1.3.1 Modeling process

The System Dynamics modeling process presented in this research was conducted in the following stages:

- 1) identification of important elements in the aquatic reservoir environment that affect fish populations;
- 2) development of the model structure to represent interacting components of the aquatic ecosystem;

- 3) establishment of causal relationships among interacting components of the aquatic ecosystem;
- 4) model refinement/model verification using data from the Limestone and Long Spruce reservoirs; and,
- 5) model use to analyze the impact of alternative reservoir management strategies on the four fish species included in the model.

1.3.2 The study area

The Limestone Generating Station (G.S.) is located on the Nelson River approximately 52 km from Gillam, Manitoba. It is the largest, most recent, and furthest downstream of five generating stations that have been developed by Manitoba Hydro on the Nelson River (Figure 1). Located further upstream on the Nelson River, generating stations have been built at Jenpeg, Kelsey, Kettle, and Long Spruce.

For the purposes of developing a simulation model to describe the reservoir environment, long-term replicated data sets, collected on a variety of physical and biological aspects of the reservoir environment each year since the project was developed, are considered ideal. Unfortunately, long-term replicated data sets are often not collected, and if collected, are often narrowly focused. However, in Manitoba, the data set collected from the Limestone reservoir has been considered the most complete data set in this province. Fisheries surveys have been completed each year since the Limestone reservoir was developed in 1989. In addition, water quality and invertebrate data has been collected intermittently from this reservoir. Also, fisheries survey data has been collected from the Long Spruce reservoir, an older reservoir developed in 1979 immediately upstream from the Limestone reservoir. Due to the similarities in location,

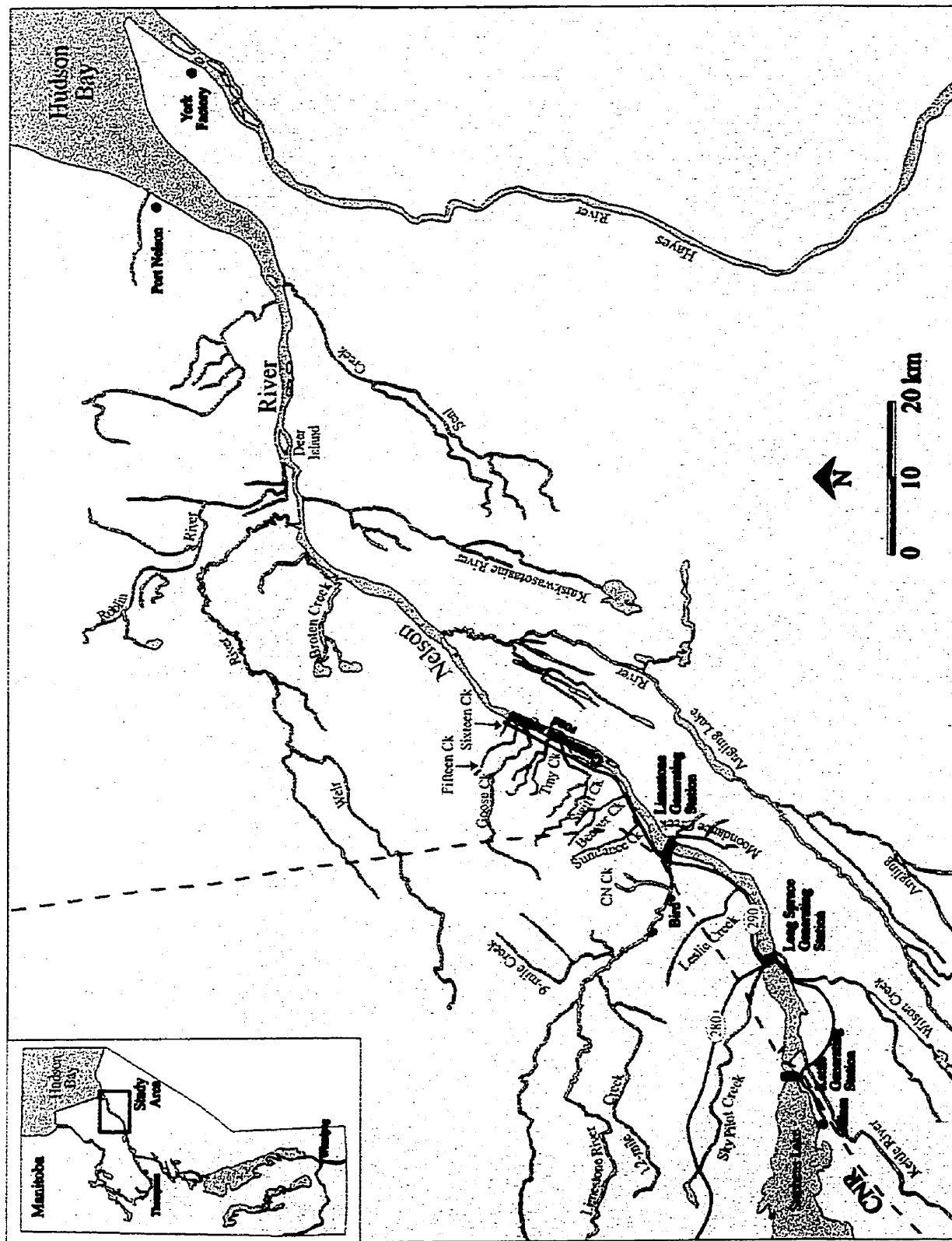


Figure 1. Map showing the location of the Limestone G.S. in relation to other hydroelectric developments on the Lower Nelson River.

size, geomorphology and biological characteristics between the Long Spruce and Limestone reservoirs, the fish populations within these reservoirs are expected to evolve in a similar manner. Therefore, fisheries survey data from this older reservoir provides a unique opportunity to compare the patterns in fish abundances as they change over time, between both reservoirs. Due to the availability of physical and biological data, the Limestone reservoir is considered an ideal case study from which to base biological predictions for future northern Canadian reservoirs (Baker 1990).

In addition to the availability of data, the Limestone reservoir is relatively small in comparison to other large reservoirs (i.e., Southern Indian Lake and Lake Winnipeg). Difficulties are encountered in monitoring and predicting the impacts of hydroelectric development and hydro operations on large reservoirs since many distinct basins and embayments may exist within these large reservoirs. The impacts of the development on each of these basins may differ considerably. Monitoring efforts may focus on one region of the reservoir, however, the data collected may not be applicable to the other reservoir regions due to differences in water depth, water chemistry, and water flow. In addition, basins within large reservoirs may differ in the fish populations which inhabit them. Focusing our initial modeling efforts on this smaller reservoir will reduce the complexity of this initial modeling effort.

1.4 Importance of the study

The model developed in this research was designed to complement past data collection and available scientific literature, with the purpose of increasing understanding and ability to make predictions concerning the effects that reservoir development and hydro operations have on fish populations. The use of a system dynamics model to

analyze the impacts of different hydro operating procedures on fish populations would be a very important and useful management tool. Application of this model to the planning process of future hydroelectric developments in Manitoba will provide, by analyzing the potential outcomes of different operating scenarios, an important tool in support of the decision making process. The local power utility, Manitoba Hydro, supported this research by providing the case study data and expertise throughout the course of this study, and financial resources for conducting the research.

1.5 Organization of the study

This thesis is organized into six chapters. The first provides a general background and overview of objectives to be met by the study, and methods for their achievement. Chapter two is a review of related literature focusing upon the physical and biological impacts of reservoir creation; and computer simulation modeling using system dynamics. Chapter three details the modeling approach and model development. Chapter four presents the results and verification of the model. Chapter five outlines the discussion and analysis of model results. Chapter six outlines the conclusions and recommendations of the study and chapter seven provides the literature cited. Special importance will be given to the identification of future research directions.

Chapter 2: Literature Review

2.0 Introduction

The literature review includes a discussion of systems thinking and system dynamics, a general overview of the physical and biological components of a reservoir which are influenced by reservoir development, a description of previous modeling efforts, and identifies trends observed in fish abundance following reservoir development. The literature review is intended to provide the reader with a background to the modeling process and the reservoir system being modeled.

2.1 Systems thinking

Resource managers are aware that research must consider the entire system and not focus on understanding only individual components of that system. The term “system” has been defined as:

“A whole which cannot be divided into interdependent parts. The system has properties that none of the parts have. A system is not the sum of its parts it is the product of their interactions. When disassembled the system loses its properties and so do its parts” (Richmond 1993).

Understanding the definition of a system is important in order to understand systems thinking. Richardson (1986) defines systems thinking as “the art and science of making reliable inferences about behavior by developing an increasingly deep understanding of underlying structure”. The benefits of systems thinking include observing how the system as a whole changes over time while increasing our knowledge about individual components of the system, and observing where limitations in our understanding of the system exist (Richardson 1986).

2.1.1 System dynamics modeling

Science has developed various methodological approaches for studying systems. One such research approach is the system dynamics approach. The system dynamics approach is closely related to the idea of systems thinking, and system dynamics and systems thinking are used almost synonymously (Ossimitz 1998). System Dynamics (SD) is a method used to describe, model and simulate dynamic systems (Ossimitz 1998). It is a computer aided approach to policy analysis, system analysis and system design. The system dynamics approach involves developing a model structure from knowledge of the system to simulate the dynamic behavior of the real world. Because real-world systems (especially ecological systems) are very complex and difficult to conceptualize, the computer aided, system dynamics approach, provides system managers with a tool that can be used to represent, analyze and understand dynamic systems. Paulik (1969) writes “because ecological systems are so complex and because the holistic approach is so important when considering the total ecological situation, ecology would seem to be a natural area for extensive application of computer simulation models”.

The system dynamics discipline was first introduced at the Massachusetts Institute of Technology by Dr. Jay Forrester to help industrial managers better understand and control industrial systems. In 1961, Forrester published “Industrial Dynamics”, the first publication in the field of SD. He developed a powerful method for describing interrelated systems (using causal loop diagrams, stock-and-flow diagrams) and the simulation language “Dynamo” for the numerical simulation of dynamic systems (Ossimitz 1998).

The system dynamics approach has experienced a major expansion over the last three decades with the advent of more powerful computers. New advances in technology provide a powerful aid for exploring the dynamics of ecosystems which has enabled resource managers to become better decision makers (Ruth 1994).

Therien (1981) and Ford (1999) describe the advantages of modeling complex systems. Therien (1981) explains that models enhance the ability to verify the response of complex interconnected systems to changes in the external environment. They provide researches with a valuable tool that can be used to identify variables or parameters that are likely to have significant effects on important biological outputs. Through their development, models provide an understanding of environmental systems and indicate where future data collection is necessary. Finally, once completed, the use of models provides the ability to predict the response of the system to time-varying inputs, allowing alternative management scenarios to be tested, and their outcomes analyzed. In addition to the above advantages, Ford (1999) explains that modeling tools can be used by developers, engineers and/or biologists, thereby initiating group discussions and improving management decisions.

2.1.2 Applications of system dynamics

System dynamics has proven to be a useful approach for addressing complex systems that change over time, be it a physical, social, biological, or economic managerial (Radzicki 1997). System dynamics has furthered scientists understanding of ecological systems. For example, single species population models, predator-prey dynamic models, and multi-species interaction models have been developed to better understand and

describe populations of wildebeast, voles, grass carp and gizzard shad, for example (Ruth and Lindholm 1996; Hannon and Ruth 1997).

Traditionally, designing and managing water resources for a variety of human uses (i.e., flood protection, stable water levels for irrigation, recreation, hydropower production) is difficult, expensive and time-consuming (Simonovic et al. 1997, Simonovic 2000). However, water resources planning has adopted (as one approach) a decision support approach based on simulation modeling using the SD methodology (Simonovic et al. 1997, Fletcher 1998). The SD methodology has aided in reducing the difficulties encountered in the water resources planning process by providing a tool that can be used to test alternative hypotheses.

Although used to manage water resources and optimize hydropower production and scheduling, application of the system dynamics approach to fisheries management is a relatively new challenge (Hannon and Ruth 1997). Previous attempts at dynamic modeling of fish populations have involved coastal commercial fisheries (Ruth 1994; Ruth and Lindholm 1996; Hannon and Ruth 1997). In these models, scenarios are run to explore the implications of viable management strategies under alternative assumptions on the driving forces behind complex ecological-economic processes (Ruth 1994). These models allow alternative management strategies such as effort controls and gear restrictions to be examined. The goal of most of these models is to develop an understanding of the fishery, and find a management strategy that will maximize sustainable yield.

The logical extension of this application of SD focuses on inland fisheries and more specifically, fish populations that are affected by reservoir development and hydro

operations. A wealth of research, monitoring and field data related to inland fisheries management and the effects of reservoir development and hydro operations on fish populations within reservoir systems is available. These data provide a good base for development of a SD model, making development of such a model a logical and valuable application.

2.1.3 Fisheries models

Fisheries managers have long been using models as tools to manage fisheries since they are valuable for the synthesis and interpretation of large quantities of data. However, the advancement in the science of predicting fisheries yields has been slow since the inception of stock-recruitment (Ricker 1975) and dynamic pool models (Beverton and Holt 1957, Freeberg et al. 1990). The dynamic pool model (Beverton and Holt 1957) and the surplus-yield model (Schaefer 1954) provide the basis for many modeling attempts. These models have been thoroughly analyzed and many variations of the basic models were developed and applied mostly to marine commercial fisheries (Schaefer 1968, Paulik 1969, Tautz et al. 1969, Pella and Tomlinson 1969, DeAngelis et al. 1977, Walter 1978). The goal of many of these models is to predict the maximum sustainable yield of a fishery from the available fisheries data. Some of the above models have been successful in predicting fisheries yields for marine commercial fish species.

Some examples of fisheries models are discussed below. Watt (1956) and Paulik (1969) presented models for inland fish populations, however, both require considerable data and mathematical expertise to use them. Orth (1975) built a largemouth bass model which does not include other fish populations. Prentice and Clark (1978) developed a systems model for walleye management, and used it to predict walleye yields from 17

reservoirs in Texas. Taylor (1981) developed a generalized fisheries simulator model that uses an age structure similar to the model developed by this thesis.

Freeman et al. (1990) writes “many of the models now in use are based on mathematical correlations between measurable characteristics of a system (e.g., stock size, spawning biomass) and offer little explanation of the mechanisms responsible for the observed condition”. This practice has produced stock-recruitment relationships with sufficient variability to raise questions as to their usefulness to fisheries management (Jacobsen and Taylor 1985). Estimates of recruitment and yield will continue to be inaccurate and unreliable until the factors responsible for variations in year-class strength are determined and incorporated into predictive models (Freeberg et al. 1990). Scientists must work to understand the mechanisms that influence fish populations, and include these in models, if models are going to be used to improve our predictive ability.

Presently, many models are available for the fisheries manager, however, many are not used for a variety of reasons (Taylor 1981).

1. The theoretical basis of many models is too complicated for the average biologist to understand. Even biologists with average knowledge of models and modeling do not apply models to manage fisheries.
2. The models are not suitable for inland fisheries (since the focus is often oceanic fisheries) and therefore, the data required, the model's framework and assumptions are not suitable to apply to an inland fishery.
3. Generalized models do not have the flexibility to apply to other systems.
4. Many models do not attempt to include density independent factors.
5. Some modeling techniques have not been computerized.

2.2 System description

2.2.1 Study area

The Nelson River is a large, fast flowing River which drains 1,072,000 km² of land area from the Rocky Mountains to within 20 m of Lake Superior (Maclaren Plansearch 1986). In addition to its natural flows, the Nelson River has been augmented by approximately 30% due to the Churchill River Diversion Project. The Churchill River diversion project was built to divert approximately 75% of the Churchill River's flow into the Nelson River. The purpose of this diversion project was to increase the hydroelectric potential of the Nelson River.

The Limestone reservoir is located on the Nelson River approximately 50 km northeast of Gillam. The Limestone reservoir is approximately 22 km long. It is defined by the Long Spruce G.S. at the upstream end, and the Limestone G.S. at the downstream end (Figure 2). Contained within the 22 km reach of the Nelson River between the Limestone and Long Spruce G.S. are four small tributaries, including Sky Pilot Creek, Wilson Creek, Brooks Creek and Leslie Creek (Figure 2).

The Limestone reservoir is located on the edge of the Precambrian shield, Hudson Bay lowlands. In the area, Precambrian Shield is overlain by Paleozoic dolomitic limestones and sandstones. Approximately 30 m of unconsolidated Quaternary sediments, marine and lacustrine silts and clays, and local deposits of glaciofluvial sands and gravels, overlie the Paleozoic rocks (Maclaren Plansearch 1986). The only relief in the area is at the Nelson River and its tributaries, with the remainder being described as flat and rolling.

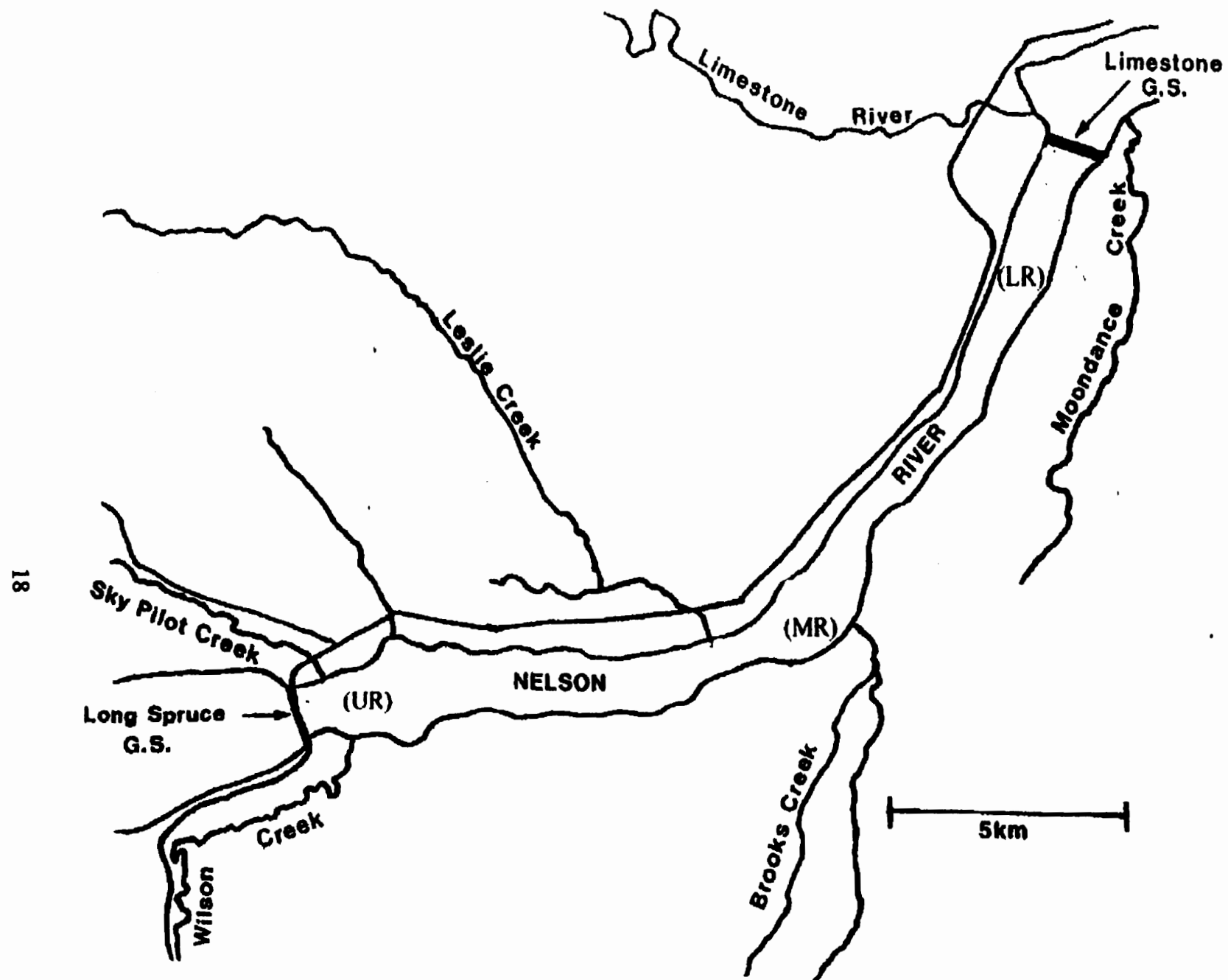


Figure 2. Location of the upper region (UR), middle region (MR), and lower region (LR) in the Limestone reservoir
(Adapted from Horne and Baker, 1993).

The climate is humid subarctic, consisting of cool short summers and long cold winters. Frost can occur during all 12 months of the year with only 13 to 70 frost-free days per annum (Penner et al. 1975). Mean annual precipitation is 32 cm (Penner et al. 1975). Due to the steep banks of the Nelson River in the area, the development of the Limestone reservoir resulted in the flooding of only a small area. Although only a small area was flooded, considerable change occurred to the flow and water regime in the newly created Limestone reservoir (Bretecher and MacDonell 1998). Water depth just above the Limestone G.S. increased approximately 30 metres, while depths just below the Long Spruce G.S. increased approximately 4 metres (depending on water levels). Water velocities also changed throughout the reservoir. For example, water velocities decreased from 2.0 - 4.0 m/sec throughout the reservoir area prior to impoundment, to 0.8 m/sec - 1.2 m/sec and 0.15 m/sec - 0.3 m/sec, in the upper and lower regions of the reservoir, respectively (depending on discharge). Because the effects of reservoir development and hydro operations depend highly on the region of the reservoir, Baker (1990) distinguished between three regions, the upper, middle and lower regions in the Limestone reservoir (Figure 2). Since physical characteristics such as depth, water velocity and water level fluctuations differ between reservoir regions, fish habitat and spawning conditions are also different between these regions. Due to these differences, the model was built to consider the different physical conditions that exist between these three regions.

2.2.2 Impacts of hydro-electric development

Reservoir environments are complex ecosystems. Construction of a hydroelectric generating station results in two immediate changes to the river environment; increased

water levels; and, changes in the natural flow regime now controlled by discharge from the hydroelectric generating station. Both these impacts consequently affect the physical characteristics of the environment, which in turn affect the aquatic biota (including fish) in the reservoir. The physical, chemical and biological impacts resulting from construction and operation of a hydroelectric generating stations have been extensively studied. The purpose of the following sections is to provide an overview of many of the important impacts.

A reservoir created from river impoundment generates a complex web of impacts which affect the human, biological, and physical components of the environment (Baxter 1977; Baxter and Glaude 1980; Petts 1984). The sudden transformation of a river, and the flooded terrestrial environment, into a lacustrine type environment, may result in changes to water depth, water velocity, water temperature, water quality, turbidity and surface area of the water body (Baxter 1977; Petts 1984; Baker and Davies 1991). Aquatic plants, plankton, benthos (bottom dwelling organisms), invertebrates, and fish are forced to adapt to these new conditions to survive (Baxter and Glaude 1980; Therien, 1981; Rosenberg et al. 1987).

A general description and sequence of biological events following reservoir development is included in Machniak (1975b). "Initially, the rise in water level floods the surrounding area and drowns the surrounding vegetation. The flooded vegetation soon begins to rot, which results in an increase in nutrients, causing further increases in plankton, flora and fauna. Fish benefit from the increased nutrient levels and food, and populations expand rapidly. However, after a period of time, nutrients are exhausted, and production slows. Water level fluctuations, as a result of the hydroelectric operations

influence levels of flora and fauna. As the reservoir stabilizes over time, various niches will be filled by different species of fish. It is generally believed that over time, the production of fish declines, due to the loss of nutrients and overall productivity". Many investigators have stated that the decline in fish production in reservoirs is due largely to changes in species composition, from an early population of mostly predators and other game species, to a population comprised of predominantly of less valuable species.

The above description is a generalization. The environmental impacts and sequence of biological changes associated with hydroelectric development will differ depending on the location of the development. The physical, biological and chemical impacts resulting from reservoir development are numerous. Macan (1963) describes a framework for the examination of impounded rivers. He separated the effects of reservoir development into first, second and third order impacts (Figure 3). First order impacts are abiotic factors that are immediately changed following reservoir development (i.e., water depth and water velocity). Second order (i.e., aquatic plants and invertebrates) and third order impacts (i.e., fish), are biotic factors that are influenced by first order impacts. Macan (1963) described a considerable time-lag between these stayed impacts (first order) and biological impacts (second and third order impacts). The time differential, Macan (1963) notes, may be a result of gradual changes in plant, insect and fish populations influenced by the modified abiotic environment.

Aquatic ecosystems are difficult to describe due to the numerous interactions between predators and prey. Figure 4 provides a link diagram of a reservoir aquatic ecosystem (Lawrence et al. 1999). This diagram shows the potential food web on an aquatic reservoir environment. Aquatic ecosystems are very complex because many fish species

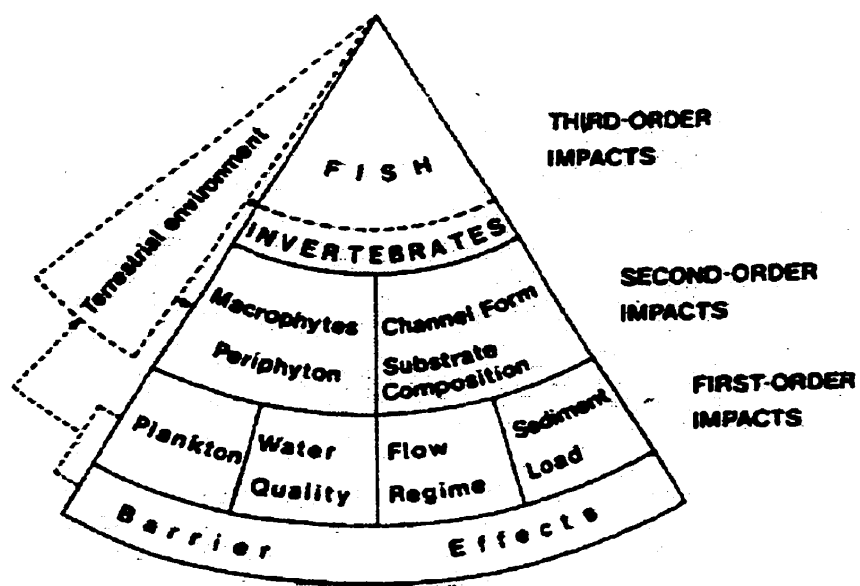


Figure 3. A framework for the examination of impounded rivers (Macan, 1963).

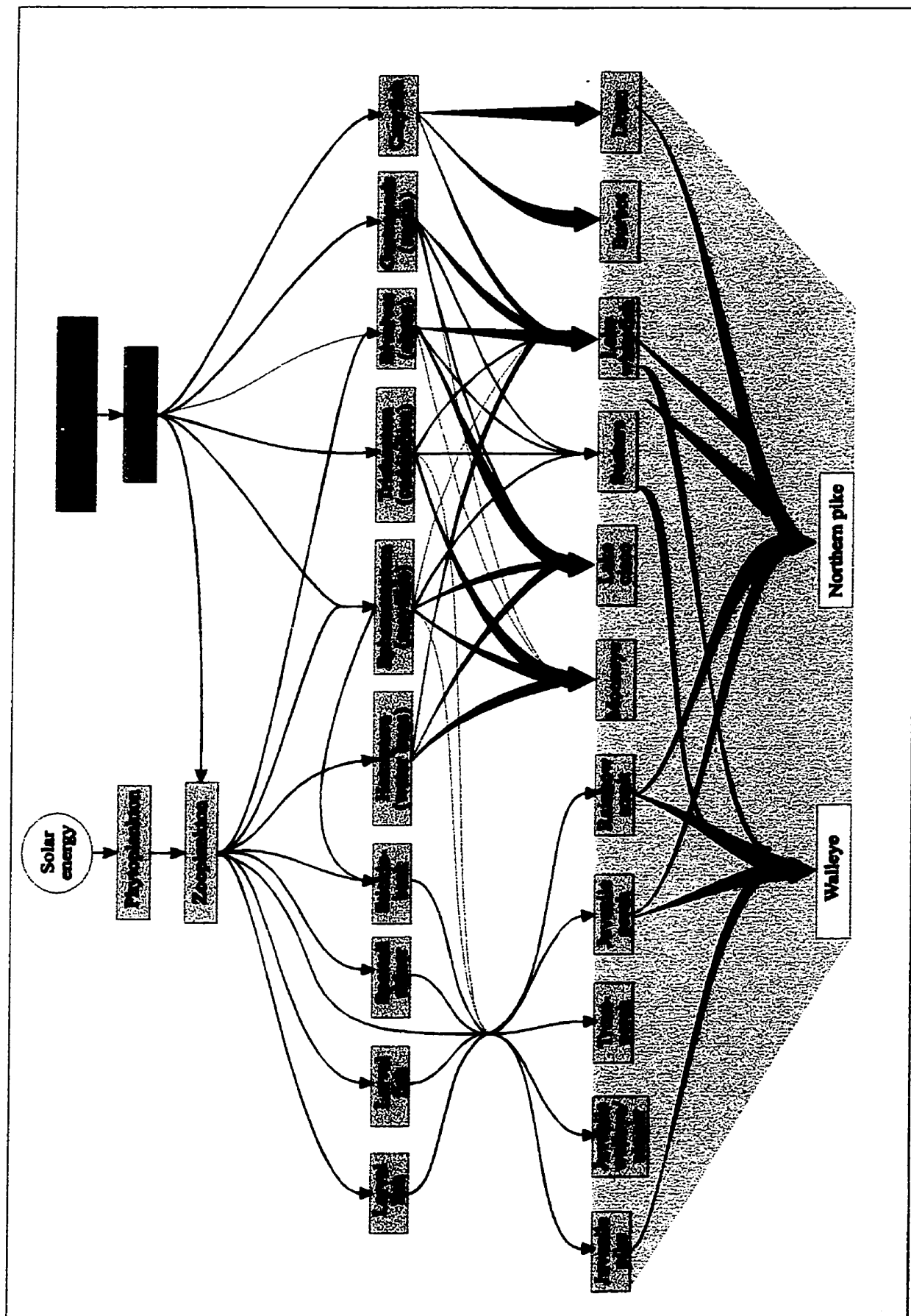


Figure 4. Food web of an aquatic reservoir ecosystem (Adapted from Lawrence et al. 1999).

change their trophic level as they grow, and cannibalism may occur. Larval fish are thought to feed primarily on zooplankton, until they grow to adequate size for consuming food items typical of their species. In the Limestone reservoir, walleye and northern pike are the major fish eating predators, while longnose sucker and lake whitefish feed primarily on a variety of invertebrates.

2.2.3 Effects of hydro operations

The impacts of hydro development go beyond the construction of generating stations and the initial raising of water levels. Daily operations of generating stations also affect the biological, physical and chemical components of the environment. For example, biological components of riverine ecosystems are adapted to the natural flow regime. They depend not only upon average flows, but also upon periods of high, low, and zero flow to satisfy requirements of their lifecycles. Periodic high flows may be important for spawning habitat, and for the recharge of floodplain wetlands. Flow regimes that are influenced by hydro operating procedures may not allow for the natural cycle of seasonal high or low flows (Baxter and Glaude 1980).

Manitoba Hydro operators decide on the rate of discharge from a hydroelectric generating station on an hourly basis. Also, hydro operators can control the water level of a reservoir from month to month or season to season. As previously discussed, both short-term fluctuations in discharge, and seasonal water levels of the reservoir exert important influences on fish populations in the reservoir environment. The next section discusses some of the impacts that short-term discharge rates, and seasonal water levels have on the reservoir environment.

2.2.3.1 Hourly discharge rates

The hydrological characteristics of a reservoir exert the fundamental controls over the biology of water system (Petts 1984). The rate at which water is discharged from the hydroelectric generating facility, and the frequency and severity of discharge variations may affect the physical, chemical and biological characteristics of a reservoir (Baxter 1977).

The time and extent of peak power demand plays an important role in determining the volume of water and time of its release from a hydroelectric generating station. In typical hydroelectric operations in Manitoba (including Limestone the case study site), water is stored in the reservoirs at night when electricity demand is low, and discharged through the turbines during the day to satisfy peak power demand. This discharge process has been described in the literature as a pulse release (Cushman 1985). Pulse releases cause frequent fluctuations in water level and water velocity downstream from hydroelectric generating stations. The magnitude and frequency of these fluctuations have important impacts on the biota of the reservoir (Cohen and Radomski 1993).

Daily fluctuations in reservoir releases fluctuate the reservoirs water levels and water velocities which can adversely affect aquatic biota, and may affect the carrying capacity of many life forms (Fisher and LaVoy 1972). Fluctuating water levels have been found to affect invertebrate drift, distribution and concentrations of organic materials, sediments, water quality and water temperature (Cushman 1985). Species of invertebrate, plant, animal and fish rely upon many of these factors for various stages of their life history. The effects of discharge variations, and the detrimental effects of pulse releases, and flow reduction on fish have been noted by several authors (Johnson 1957,

June 1970, Edwards 1983, Cohen and Radomski 1993). Among the numerous impacts of fluctuating water levels are disruptions to spawning success and spawning migrations of many fish species, stranding of fish and fish larvae, loss of habitat, and reductions in the number of rooted plants (Inskip 1982, Gaboury and Patalas 1984, Masse et al. 1993).

The amount and timing of water discharged from hydropower developments during pulse releases are important consideration when evaluating the impacts of hydro developments on aquatic biota in the reservoir. However, with the exception of a few studies on the impact of water level fluctuations on fish spawning conditions and fish habitat in hydroelectric reservoirs, the effects of pulse releases on aquatic life in Canadian waters have received little attention (Cushman 1985).

2.2.3.2 Seasonal water levels

Seasonal water levels are also an important consideration for an aquatic ecosystem. For example, seasonal water levels may influence various life-history stages of fish, since fish life-history events are seasonally timed. Gaboury and Patalas (1984) found that low water levels during spring prevented pike and walleye from accessing important spawning areas. In nature, water levels are normally highest during spring when winter run-off increases water levels, and lowest during winter, when water levels are low due to decreased inputs from precipitation.

In many Manitoban reservoirs, the development and operation of the reservoir changes the natural occurrence of events. This is because power suppliers operate to store water in reservoirs during summer, and increase discharge rates during winter when power demand is highest. The increase in discharge results in the lowering of water levels in the reservoir, termed “winter drawdown”. Winter drawdown can seriously

impact certain species of fish. For example, on Cross Lake, winter drawdown has negatively affected the year-class strength and abundance of fall spawning fish species such as lake whitefish and lake cisco (Bodaly et al. 1984a, Gaboury and Patalas 1984).

Many reservoirs in Manitoba are drawn-down during winter to supply the increased demand for power. Examples include: Cross Lake, Southern Indian Lake and Lake Winnipeg (Rosenberg et al. 1987). However, the Limestone reservoir is an exception. In Limestone, water levels have been held fairly uniform since 1989 on a seasonal basis, and winter drawdown has not occurred. Although seasonal fluctuations are minimal, water levels fluctuate on an hourly basis.

The purpose of the model developed in this research was to determine what type of water level management may work to improve conditions for fish in reservoirs. To solve the problem of optimal timing and release of water from reservoirs, Plosky (1986) discussed the results of over 350 papers relating the effects of water level changes to aquatic biota. He stated that in order to maximize benefit to aquatic biota in a reservoir system, most managers should seek to: (a) draw down water levels in late summer or fall, (b) establish terrestrial vegetation by seeding or allowing for recolonization, (c) flood vegetation in the spring, and (d) maintain high water for as much of the growing season as possible.

Similarly, Groen and Schroeder (1978) report that manipulation of water levels have proven to be a valuable tool for the fisheries manager. They describe a seasonal water level management plan (similar to Plosky (1986)) that will improve fisheries within hydroelectric reservoirs (Figure 5). This cycle is as follows:

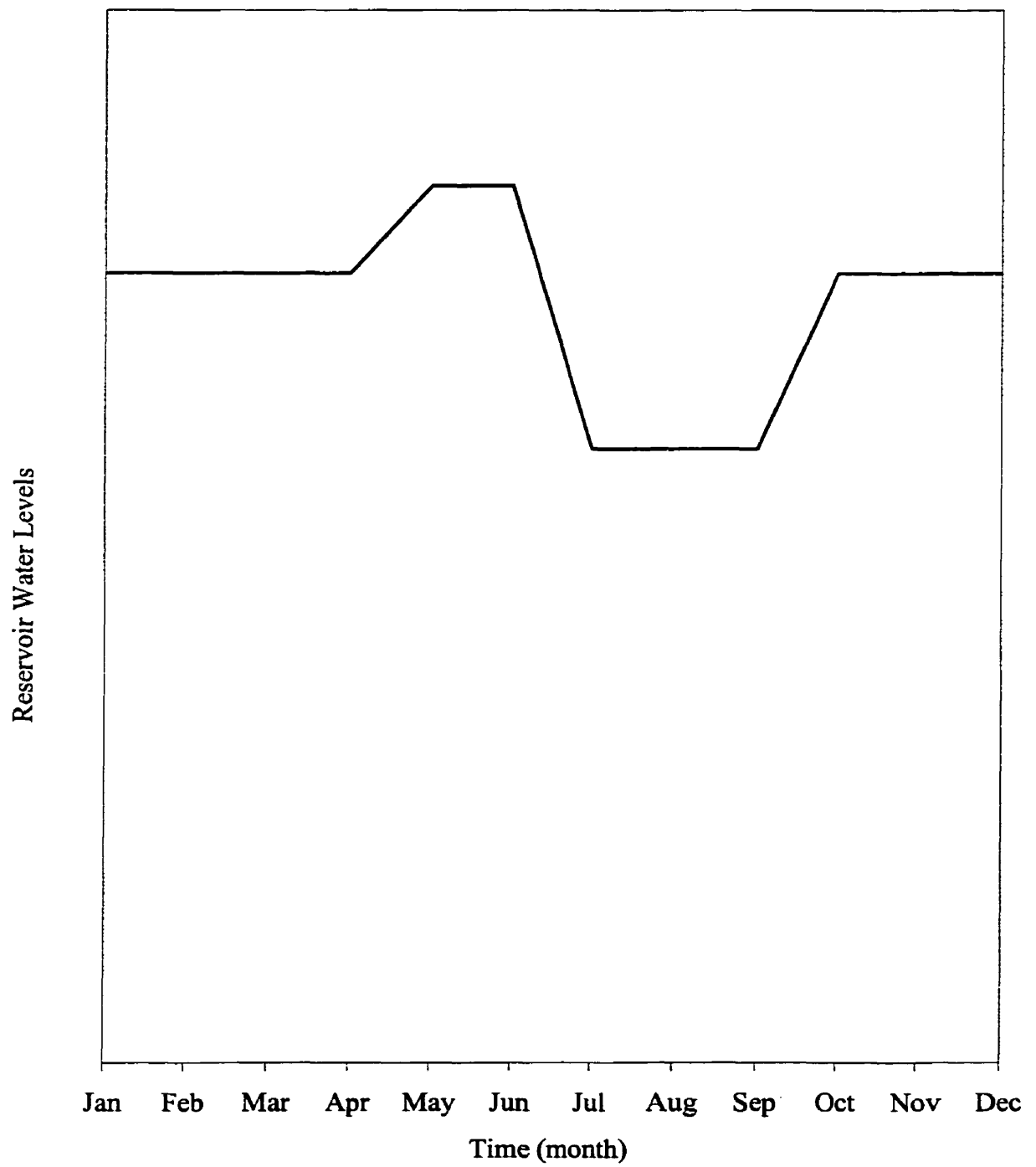


Figure 5. Proposed monthly reservoir water level management plan.
(Source: Groen and Schroeder 1978, Plosky 1986).

- 1) Gradually raise water levels in the spring, prior to fish spawning, to flood vegetation and rocky areas.
- 2) Keep relatively stable or rising water levels through late spring, to provide favourable nursery habitat and to flood vegetation.
- 3) Around mid-summer drawdown the reservoir to expose inundated areas for re-vegetation.
- 4) During late fall, raise water levels to flood the area exposed during mid summer drawdown.
- 5) Stabilize water levels during winter.

These water level management plans can be tested by the model developed in this research. The discharge from a hydroelectric generating station, results in both short-term water level fluctuations and can impact the water level in the reservoir on a seasonal basis. Both short-term water level fluctuations and seasonal water levels impact fish populations within a reservoir in a variety of ways. These impacts will be discussed in relation to each fish species included in the model in Chapter 3.

2.3 Reservoir water quality

Baxter and Glaude (1980) and Therien (1981) discuss that the impoundment of a river may alter the water quality of the reservoir. There are several different ways that water quality could be altered in response to reservoir formation, including: increased erosion or increased water turbidity, changes to nutrient levels, primary productivity and temperature which will be discussed in greater detail in subsequent sections.

In some reservoirs, increasing air temperature as summer approaches raises water temperature which may result in the stratification of a reservoir into three temperature

layers (Wetzel 1983). In a cascading reservoir system, stratification of the reservoir could result in temperature differences from the water released from upstream reservoirs into downstream reservoirs, which may have adverse effects on aquatic biota. However, the Limestone and Long Spruce reservoirs do not experience thermal stratification due to short retention times (four days), and thus potential for adverse effects due to water release from a stratified reservoir are avoided (Horne and Baker 1993).

Water quality data has been collected from the Long Spruce reservoir, the Limestone reservoir and unimpounded lower Nelson River in 1990, 1991, 1992, 1993, 1994, 1996, and 1999. These data were used to facilitate comparisons between an older reservoir (i.e. Long Spruce), younger reservoir (i.e. Limestone reservoir), and unimpounded lower Nelson River (Zrum and Kennedy 2000). Water quality parameters that were measured during these studies include: nutrients (nitrogen, phosphorus and carbon), chlorophyll *a*, and total suspended solids. Included in the following sections are the results of these and other studies discussing the effects of reservoir development and hydro operations on these water quality parameters.

2.3.1 Nutrients

Typically, most reservoirs exhibit an initial upsurge in nutrients immediately following impoundment as a result of the large influx of organic and inorganic material from the inundated terrestrial environment (Baxter 1977; Petts 1984; Kimmel and Groeger 1986). This nutrient upsurge may stimulate an increase in both primary and secondary productivity, which, in turn, may encourage an increase in the population of some fish species (Figure 6) (Machniak 1975b; Kimmel and Groeger 1986). Many authors detail a decrease in reservoir nutrient levels 2-3 years after impoundment due to

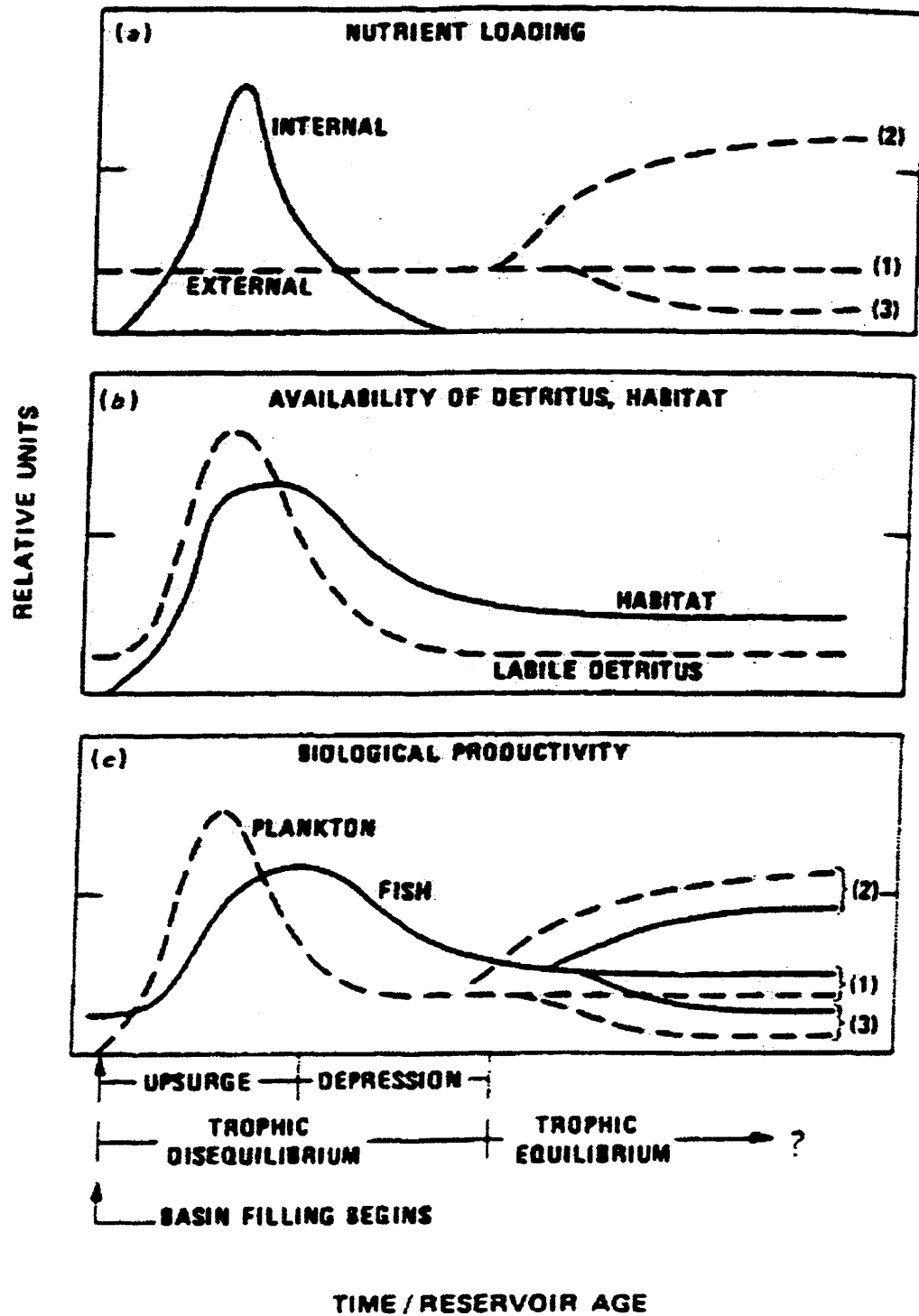


Figure 6. Changes in factors influencing reservoir water quality and biological productivity as a reservoir ages: (a) internal and external nutrient loading, (b) availability of fish and invertebrate habitat, and (c) plankton and fish production (Kimmel and Groeger, 1986).

reduced internal nutrient loading, and the degradation of flooded vegetation (Machniak 1975b, Baxter 1977; Kimmel and Groeger 1986). Depressed nutrient levels may last 25-30 years at high latitudes but may last only 6-10 years at lower latitudes (Machniak 1975b). Decreasing nutrient levels are believed to contribute to a decrease in primary and secondary productivity, as well as a decline in fish productivity (Figure 6) (Kimmel and Groeger 1986).

Elevated nutrient levels that have occurred immediately following impoundment and the associated rise in biological productivity has often produced false hopes for a higher level of fisheries production than can be sustained. Given these findings, it seems apparent that the productivity level or fish yield during the initial phase of a reservoirs existence should not be used as a basis for formulating long-term management strategies (Doan 1979).

Nitrogen, phosphorus and carbon have been measured in the Long Spruce reservoir, Limestone reservoir and unimpounded Nelson River intermittently since 1989. These data were collected to facilitate comparison between reservoirs of different ages, and the unimpounded Nelson River. Analyses of these data suggest that nutrient levels have remained relatively unchanged following impoundment of the Limestone reservoir and that nutrient levels are relatively similar between the Long Spruce reservoir, Limestone reservoir, and unimpounded Nelson River (Zrum and Kennedy 2000).

The reasons why nutrient levels in the Limestone reservoir did not follow the pattern observed in other reservoirs is unknown. Petts (1984) suggested that reservoir nutrient levels in a cascading reservoir system are influenced by water releases from an upstream generating stations, and that sediments may settle out in the slow moving lower reservoir

region, causing water releases from upstream reservoirs to be low in nutrients. Another reason why nutrient levels may not have become elevated with the development of the Limestone reservoir is because a large amount of land area was not flooded in the creation of the Limestone reservoir. Therefore, a large influx of nutrients normally associated with the flooding of large amounts of land after reservoir development did not occur (Maclaren/Intergroup 1986).

2.3.2 Primary Productivity (chlorophyll *a*)

Chlorophyll *a* is a photosynthetic pigment in algae and plants. It is used as a measure of water quality to estimate phytoplankton biomass in the water column. Measuring the amount of chlorophyll *a* in the water column gives the researcher an estimate of primary productivity, an indicator of the productivity of the lower levels of the food chain.

Kimmel and Groeger (1986) discuss that increased nutrient levels that normally occur following impoundment may produce an increase in primary productivity. However, since development of the Limestone reservoir, chlorophyll *a* levels, like nutrient levels, have not changed substantially (Zrum and Kennedy 2000). Additionally, Zrum and Kennedy (2000) compared chlorophyll *a* levels in the Limestone reservoir with the unimpounded section of Nelson River, and the older, upstream reservoir Long Spruce. Results suggest that chlorophyll *a* levels have remained relatively similar between all three sites since monitoring began in 1989.

2.3.3 Total suspended solids

Concentrations of total suspended solids (TSS) influences light penetration, the depth to which photosynthesis can proceed, and visibility of sight feeding fishes (Baxter and Glaude 1980). Under natural conditions, concentrations of total suspended solids in the

water column has been strongly correlated with discharge, and in most cases reflects seasonal flow variations (Petts 1984). Impoundments usually work to change the natural flow and discharge regime. For example, reservoir environments immediately upstream of an impoundment provide areas of low current velocity, which allows sediment held in suspension to settle out. Therefore, water releases in a cascading reservoir system may be associated with reduced levels of total suspended sediment (Hales et al. 1970).

Hecky et al. (1984) found that total suspended solids in the water at Southern Indian Lake, Split Lake, Sipiwesk Lake, Cross Lake, and Norway House increased due to increased water levels and water flows down the Nelson and Burntwood rivers following the development of the Churchill River Diversion Project. Playle and Williamson (1986) discuss that higher water flow may have increased the level of erosion, which increased concentrations of total suspended solids in the water.

Elevated water levels and higher water flows which increase the amount of erosion, have been considered the causal factor behind increases in the amount of total suspended solids in the water column (Petts et al. 1984, Kimmel and Groeger 1986). Water levels were raised nearly 30 m in the lower region of the Limestone reservoir, however, less than 3 km² of land area was flooded (MacLaren/Intergroup 1986). Data from the Limestone reservoir suggests that the TSS levels in the water column were elevated for only one year, before decreasing to levels which are comparable to the Long Spruce reservoir (Zrum and Kennedy 2000). Zrum and Kennedy (2000) compared total suspended solid data between the Long Spruce and Limestone reservoirs and the unimpounded lower Nelson River. The data indicates that measurements of total suspended solids in both reservoirs were lower than those observed in the Nelson River.

2.4 Fish diet

The amount of forage available for fish in reservoirs is expected to affect the abundance, survival rate and carrying capacity of fish populations in reservoirs. This thesis considers invertebrates, forage fish, zooplankton and smelt as the main components of fish diet. A monitoring plan designed to determine the impacts of hydroelectric development on fish populations should consider these components of fish diet. The purpose of the following section is to describe impacts that reservoir development and hydro operations may have on the components of fish diet.

2.4.1 Invertebrates

Invertebrates are an important food source for certain fish species, including two of the species included in the model, lake whitefish and longnose sucker. The lifecycle of many invertebrate species are related to the natural seasonal variations in discharge and temperature. Some invertebrate species are limited in their preference of water depth, and the short term magnitude and frequency of flow variations (Fraser 1972). Petts et al. (1993) found that periods of extreme low and high flows were related to decreases in invertebrate populations.

The impact of impoundment on invertebrates has varied depending on the reservoir. Following impoundment at Southern Indian Lake, invertebrate populations initially increased in number, remained high for a few years, and then decreased to near pre-impoundment levels (Giberson et al. 1992). This was thought to be caused by an initial nutrient increase resulting from flooding, and a subsequent depletion of nutrients once the organic matter began to decay. However, further study found that the population

dynamics were strongly correlated to air temperatures, rather than hydroelectric development.

Weins and Rosenberg (1994) surveyed benthic invertebrates in 12 Manitoba lakes affected by the Churchill River diversion project. Invertebrates were surveyed prior to the development of diversion project in 1976, and then every two years after the diversion was developed, until 1987. In lakes dewatered by the Churchill River diversion, benthic invertebrate standing crop declined to about 25% of pre-impact values. In lakes formed by the diversion project, where water levels were raised, benthic invertebrate standing crop was found to have increased and remained high. The authors attributed this to the influx of nutrients from the diverted Churchill River into these lake basins.

Baker and Schneider-Vierra (1993) compared the invertebrate populations immediately following construction of the Limestone Generating Station in 1990, to populations in the Limestone, and Long Spruce reservoirs in 1992. In the Limestone reservoir, flooding initially reduced total invertebrate numbers, and the scale of reduction was correlated to the severity of flooding. However, by 1992, invertebrate populations had become re-established in the Limestone reservoir, and total numbers were half of those found at undisturbed control sites in the Long Spruce reservoir and Nelson River mainstem. Zrum and Kennedy (2000) discuss that the invertebrate productivity in the Limestone reservoir in 1999 has increased in comparison to previous years. In fact, invertebrate numbers in 1999 were the highest recorded since the monitoring program was initiated in 1989.

2.4.2 Rainbow smelt

Rainbow smelt (*Osmerus mordax*) were first captured in Lake Winnipeg in 1990 (Campbell et al. 1991) and the Limestone reservoir in 1996 (Remnant et al. 1997). The colonization of rainbow smelt in an aquatic ecosystems is usually accompanied by changes to the fish community. Rainbow smelt affect other fishes by predation on their young, but also by changing food web structures (Evans and Loftus 1987). There is evidence of restructuring of zooplankton and forage fish communities following introduction of smelt (Crowder 1980, Siegfried 1987, Evans and Loftus 1987). Also, growth rates of piscivorous fish species, such as walleye and pike, have been noted to increase (Bridges and Hambly 1971, Hiltner 1983, Evans and Loftus 1987, Ryan and Kerekes 1988). High correlations between declines of lake whitefish and increasing rainbow smelt populations have been shown in many aquatic ecosystems (Anderson and Smith 1971, Christie 1972, 1974, Crowder 1980). Several authors have suggested that predation by rainbow smelt on coregonid larvae or competition for food and space has played an important role in the coregonid declines (Anderson and Smith 1971, Crowder 1980, Loftus and Hulsman 1986, Evans and Waring 1987).

Competition between rainbow smelt and native coregonids and other species has been implicated but not researched in many studies. Most studies focusing on the interaction between lake cisco, lake whitefish and rainbow smelt have relied on circumstantial or correlative evidence whereby population data on each species are compared from year to year (Wain 1993). Evans and Waring (1987) inferred competition between rainbow smelt and lake whitefish in Lake Simcoe by the decline of lake whitefish during high

rainbow smelt abundance. Evans and Loftus (1987) suggested that the negative correlation between cisco, lake whitefish and rainbow smelt abundance, combined with the similar niche requirements of each species, implied competition. Wain (1993) examined two small lakes in the Winnipeg River drainage basin on Northwestern Ontario and found negative impacts to lake cisco, lake whitefish, and yellow perch populations, which was believed to be due to competition.

Data from stomach content analyses of fish in the Limestone reservoir in 1999 indicates a substantial change in fish diets since monitoring of the fish populations began in 1989 (Bretecher and MacDonell 2000). In 1999, rainbow smelt comprised 70% and 52% of northern pike and walleye diets in the Limestone reservoir, respectively. Prior to 1996, no rainbow smelt were found in pike or walleye stomachs.

While further research is required to understand the apparent effects of smelt reservoir ecosystems in Manitoba, it is clear that smelt have important community wide impacts on that should be considered important for environmental managers.

2.4.3 Zooplankton

Measures of zooplankton abundance are important indicators of secondary productivity to biologists. Ware (1975), Morrow et al. (1997) (and others) discuss that zooplankton abundance and availability is very important to the survival of many fish species during the larval stage of their development because they are an important food source. In the literature, zooplankton abundance has been associated with nutrient levels and chlorophyll *a* levels (Machniak 1975(b) Kimmel and Groeger 1986). Zooplankton abundance has not been measured in the Limestone reservoir since impoundment.

2.5 Fish and fisheries

Following impoundment, fish populations in a newly created reservoir must adapt to changes in: a) the physical and chemical conditions of the reservoir; b) available food; and, c) spawning conditions (Machniak 1975b). Factors that influence how a fish species adapts to these changes will determine their success in the reservoir.

Hydro operations and reservoir development have been discussed as key factors which influence these conditions, and thus abundance of many fish species in reservoirs (Machniak 1975, Baxter and Glaude 1980, Bietz 1988). Successful reproduction under the new aquatic conditions created by reservoir development may create great challenges for some fish species, while benefiting others. Fish reproductive success or young of the year survival has been linked directly to impacts or changes induced by reservoir operations.

Baker (1990) discusses the results of fisheries surveys completed in 1989 in the Limestone reservoir. Thirteen fish species were captured during the fisheries survey, which included: longnose sucker (*Catostomus catostomus*), burbot (*Lota lota*), white sucker (*Catostomus commersoni*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), lake cisco (*Coregonus artedii*), lake sturgeon (*Acipenser fulvescens*), shorthead redhorse (*Moxostoma macrolepidotum*), sauger (*Stizostedion canadense*), walleye (*Stizostedion vitreum*), yellow perch (*Perca fulvescens*), mooneye (*Hiodon tergisus*), and silver lamprey (*Ichthyomyzon unicuspis*). Longnose sucker comprised 91% of the catch followed by burbot 2.8%, white sucker 1.5%, lake whitefish 1.4%, and northern pike 1.0%. The remaining fish were captured at less than a one percent frequency. Fisheries surveys were also completed in the Long Spruce reservoir in 1989

(Baker et al. 1990). Baker (1990) found that the species composition of the catches between the two reservoirs were different. In the Long Spruce reservoir, northern pike, white sucker, lake whitefish, longnose sucker and walleye comprised 22.4%, 21.9%, 18.7%, 7.7% and 3.4%, respectively (Baker et al. 1990).

Four fish species, lake whitefish, northern pike, walleye and longnose sucker were selected to be included in the reservoir model for a variety of reasons. First, each of the fish species are commonly found in the majority of lakes, rivers and reservoirs across Canada, including the Limestone reservoir. Secondly, trends have been observed in the abundance of each fish species following reservoir development. Thirdly, each fish species are known to experience impacts owing to reservoir development and operation of hydroelectric generating facilities. Finally, the diets of the fish species included in the model differ. Northern pike and walleye are primarily piscivorous, feeding on fish; while whitefish and longnose suckers are considered benthivores, feeding on invertebrates (Scott and Crossman 1973, Knight and Vondracek 1993, Bretecher and Macdonell 1998).

The following sections discuss some of the available literature for northern pike, lake whitefish, longnose sucker and walleye. The review is aimed at describing the spawning and feeding requirements of each species, the general trends that have been observed in their respective populations following impoundment, and the factors which may contribute to those trends.

2.5.1 Northern pike

The northern pike has a circumpolar distribution in the northern hemisphere, and is one of the few species that can be said to occur throughout Canada (McPhail and Lindsey 1970, Scott and Crossman, 1973, Inskip 1982). In Canada, the northern pike is

considered a valuable commercial and sport fish. Northern pike are spring spawners, usually spawning over submerged vegetation (Hassler 1970, Bodaly and Lesack 1984, Casselman and Lewis 1996). They are considered to be a top predator in an aquatic ecosystem, feeding mostly upon fish (Frost 1954, Lawler 1965, Diana 1979). Diet of northern pike has been shown to change with age, and northern pike have been shown to feed opportunistically on what is available in the ecosystem (Svirskaya and Ivanova 1990, Sammons et al. 1994).

The effects of hydro developments on northern pike have been extensively studied. Machniak (1975a) compiled literature from around the world to describe the impacts between changes in physical parameters (i.e., water levels, total suspended solids) on the population size, growth, feeding, distribution and movement of northern pike. Also, Machniak (1975a) describes factors which influence pike reproductive success including water temperature, water levels, spawning substrate, water quality, and predation.

Northern pike populations in reservoirs typically increase immediately following impoundment and subsequently decline to levels slightly above their initial population level. Lesack and Bodaly (1984) describe an initial increase in pike production in Wupaw Bay on Southern Indian Lake, in the year following impoundment. After the first year, pike production in Wupaw Bay decreased which the authors believe may have been due to the cannibalism of pike juveniles by the initial strong year class of pike. Similar trends have also been observed in pike populations within the reservoirs of the La Grande complex, Quebec. Here, spawning success and young of year survival increased for a period of three years following impoundment (Deslandes et al. 1994). Deslandes et al. (1994) attributed the improvement in recruitment not only to the abundance of flooded

vegetation, but also to the general increase in secondary productivity that occurred following impoundment (Deslandes et al. 1994). Fisheries survey data from the Limestone reservoir also indicates that the northern pike population followed the trend described by the literature. Initially, northern pike increased in abundance and subsequent monitoring data has shown a slow decrease over time (Baker 1990; Bretecher and MacDonell 2000). Data from the Long Spruce reservoir indicates no clear trend in the abundance of northern pike (Bretecher and MacDonell 2000).

A variety of factors have been identified as responsible for the trend observed in northern pike populations following impoundment. For example, the increase in abundance has been attributed to rising water levels which flood vegetation over adjacent land creating important spawning and nursery areas for northern pike (Holcik 1968, Hassler 1970, Machniak 1975a, June 1976, Doan 1979, Bodaly and Lesack 1984, Strange et al. 1991). In the years following the initial increase in northern pike abundance, northern pike production typically declines slowly to levels slightly above initial levels prior to impoundment (Machniak 1975a, Kupchinskaya 1985, Deslandes et al. 1994). This subsequent decrease in pike production has been attributed to the degradation of the submerged vegetation that, following the first few years of flooding, no longer provides adequate spawning or nursery habitat (Kuznetsov, 1980; Benson, 1980; Bodaly and Lesack 1984). Despite the well documented trend that northern pike decline after the flooding of a reservoir, Doan (1979) found that northern pike yields did not decrease in Cedar Lake, Manitoba following the initial increase in yield.

Northern pike abundance has also been considered as becoming dependant upon the nature of the reservoirs operation. High and rising water levels during the spring have

been shown to increase spawning success in reservoirs well after impoundment. Benson (1980) and Gaboury and Palatas (1984) related pike spawning success to increased access to spawning habitat associated with high waters during spring in Cross Lake, Manitoba. Conversely, low or dropping and fluctuating water levels have been shown to reduce pike spawning success (Johnson 1957, Wajdowicz 1964, June 1970, Machniak 1975a, Casselman and Lewis 1996).

Since much of the literature was used as a basis for many relationships used in development of the model, a further description of the literature as it relates to northern pike is provided in Chapter 3.

2.5.2 Longnose sucker

The longnose sucker is found throughout Canada (McPhail and Lindsey 1970). Longnose sucker are spring spawners, usually spawning in streams, but are also known to spawn in shallow areas of lakes and reservoirs (Scott and Crossman, 1973, Edwards 1983). Longnose sucker feed off the bottom, largely on benthic invertebrates (Rawson and Elsey 1948, Scott and Crossman 1973, Barton 1980 and Baker 1990).

Following reservoir development, the longnose sucker has been found to dramatically decrease in abundance (Deslandes et al. 1994 and Bretecher and Macdonnel 1998). A variety of factors have been discussed as influencing this decreasing trend. Ryan (1980) and Edwards (1983) discuss that water level fluctuations during the egg incubation period may decrease spawning success since longnose sucker are known to spawn in shallow water. Also, an increase in northern pike predation following impoundment has also been discussed as a factor contributing to the decreasing trend (Colby et al. 1987, Cook and Bergsen 1988).

DesLandes et al. (1994) describe decreases in longnose sucker populations following impoundment in the LaGrande Complex, Quebec. The decrease in yield was thought to be due to an increase in the pike population which prey upon longnose suckers, increased competition with the larger whitefish population, and the absence of suitable tributaries for reproduction.

In the Limestone reservoir, the longnose sucker has been the most prevalent fish species captured since 1989. In 1996, longnose suckers comprised 54.9% of the catch from the Limestone reservoir, and comprised only 8.9% of the catch from the Long Spruce reservoir (Bretecher and Horne 1997). The authors explain that most longnose sucker captured during the 1996 Limestone fisheries survey, were recruited to the population prior to reservoir development in 1989. The authors hypothesize that the differences in catch between these two reservoirs is due to a decrease in the amount of recruitment to the longnose sucker population in the years following impoundment. The authors believe that once the older year classes of longnose suckers die off, the abundance of longnose sucker in the Limestone reservoir may decline and may become less prevalent in the reservoir (Bretecher and MacDonell 1998). A further description of the literature as it relates to the longnose sucker is provided in Chapter 3.

2.5.3 Lake whitefish

The lake whitefish is considered the most valuable fish species in Canada (Scott and Crossman 1973). It is valued not only commercially but is frequently considered a highly valuable source of food to native people. The lake whitefish is considered a benthic feeder, usually feeding on a variety of invertebrates, molluscs and gastropods (McPhail and Lindsey 1970, Scott and Crossman 1973). Lake whitefish are fall spawners,

broadcasting their eggs over a variety of substrates at a variety of depths (Machniak 1975b).

Machniak (1975b) discussed some of the factors that may influence whitefish populations following hydroelectric development. Factors such as temperature, wind, turbidity, pollution, water level fluctuations, food availability and predator abundance were identified as factors which may affect whitefish populations in reservoirs.

The large number of factors that could potentially impact whitefish populations following impoundment make it difficult to predict the effect of hydroelectric development on their populations (Christie 1963, Bietz 1988). A wide variety of trends have been observed in whitefish populations following reservoir development. DesLandes et al. (1994) reported an increase in the abundance of lake whitefish following development of the La Grande complex. The authors attribute this increasing trend to the increase in primary and secondary productivity, and the increase in water clarity that occurred following impoundment. Deslandes et al. (1994) noted that immediately following impoundment whitefish abundance was slow to increase. The authors believe that this may have been due to the concurrent increase in the abundance of pike populations soon after impoundment. Deslandes et al. (1994) observed that the lowest proportion of small whitefish coincided with the highest yields of pike, which the authors believe indicated a high degree of predation by pike on young whitefish.

Doan (1979) compared pre and post impoundment commercial whitefish catches from Cedar Lake, Manitoba. He reports "The whitefish catch in Cedar Lake had been declining for about 7 years immediately preceding flooding, remained low for 3 years

following flooding, and then started to increase greatly until it averaged 3.9 times the pre-flooding harvest”.

Opposite to the above trends in whitefish abundance, reservoir development which resulted in fluctuating water levels at Cross Lake, Manitoba have been shown to negatively impact whitefish populations. Here, whitefish year class strength was negatively correlated to the extent of winter draw-down (Gaboury and Patalas 1984). Since reservoir development, the whitefish fishery on Cross Lake has diminished (Gaboury and Patalas 1984).

Fisheries survey data from the Limestone reservoir suggests no clear trend in whitefish abundance following impoundment of the Nelson River (Bretecher and MacDonell 2000). Fisheries survey data from the older Long Spruce reservoir suggests that whitefish abundance may have decreased since 1989 (Bretecher and MacDonell 2000). The literature discussed above indicates that the impact of reservoir development on lake whitefish is highly site specific, and may be dependant upon wide variety of factors. A further discussion of the literature as it relates to lake whitefish is discussed in Chapter 3.

2.5.4 Walleye

The walleye is common to most lakes and rivers throughout North America (Scott and Crossman 1973). In Canada, this fish species is valued both commercially and for sport. Walleye are considered to be piscivorous, size selective predators, preferably feeding upon soft rayed fish species (Parsons 1971, Nielsen 1980, Knight et al. 1984, Ritchie and Colby 1988). Walleye are spring spawners, preferring a gravel substrate upon which to spawn.

Generally, the trend that has been observed in walleye abundance following impoundments is the reverse of that observed in northern pike. Walleye abundance in reservoirs is usually slow to increase, but increases greatly as the reservoir ages (Jenkins 1970, Bennet and McArthur 1990). A variety of factors including predation, food availability, fluctuating water levels, spawning substrate, water levels and cannibalism have been discussed as factors influencing walleye populations in reservoirs (Priegel 1970, Chevalier 1973, Machniak 1975c, Bietz 1988).

Suitability and availability of spawning habitat has been discussed as the most important determinant influencing the trend observed in walleye abundance in impoundments. Erickson (1972) stated that the substrate in a reservoir requires five or more years of wave washing action to produce clean gravel bars, suitable for walleye reproduction. Jenkins (1970) and Bennett and McArthur (1990) correlated reservoir age to an increase in walleye numbers following impoundment was due to an overall improvement in the quality of spawning substrate.

Doan (1979) describes an increase in the abundance of walleye in Cedar Lake, Manitoba for the first six years after flooding, and reports that they continued to increase greatly 15 years after impoundment. Similarly, Bretecher and MacDonell (2000) discuss that the abundance of walleye in the Limestone, Long Spruce and Kettle reservoirs has increased dramatically since monitoring began. In the Limestone reservoir, walleye appeared to be increasing in abundance since the reservoir was developed in 1989, and 10 years after the reservoir was developed comprised nearly 22% of the total catch. In the older Long Spruce reservoir, walleye were the most frequent species captured in fisheries surveys in 1996 and 1999, and were the second most frequent species captured in the

Kettle reservoir in 1996 (Bretecher and Horne 1997). A further description of the literature as it relates to walleye is provided in Chapter 3 – model development.

2.6 Conclusions

Obviously, a large number of interconnected factors influence fish populations in reservoirs. When planning and predicting the impacts of new developments it is important to identify and consider as many of the factors as possible. This will help resource managers to identify conditions that may have positive impact on fish populations in reservoirs. Also, it will help biologists and hydroelectric developers better understand the effects that reservoir development and hydro operations have on fish, which will hopefully lead to better management decisions (Hansen et al. 1998).

Chapter 3: Methods

3.0 Introduction

Understanding and predicting how fish populations may be affected by hydroelectric development and hydro operations is a difficult task. Representation of a natural ecosystem through the use of models with a high degree of accuracy is also difficult. Our ability to develop a model of the natural ecosystem is limited by our understanding of the system, by our limited capacity to include all the interactions that take place in the system, and by our ability to account for the influence of factors that are beyond our control (i.e., weather) (Hannon and Ruth 1997). For these reasons, the goal of a model (applied to a biological system) cannot be a complete, precise representation of the actual system.

The goal of many models, including the model developed by this research, is to generally represent the behaviour of a system and to allow the model user to investigate alternative scenarios. Through the development of the model, and through the investigation of various scenarios, a model helps interested parties develop a better understanding of the system. Also, by identifying important interactions that are poorly understood, the model user gains insight into the dynamics of the system (Ford 1999). It is hoped that the model developed by this research will further the understanding and ability to prediction of the impact of hydro development on fish populations.

The preceding model user and reader of this thesis should understand that some of the relationships used in development of the model should be regarded as tentative and open to modification. Prospective users should understand that the relationships are not the products of extensive laboratory or scientific investigations. Rather, they reflect the

author's subjective integration of the literature and personal experience. In addition, for the future applicability of this model, it should be understood that not every reservoir is similar physically, chemically and biologically, and that the physical, chemical and biological interactions that take place in a reservoir, will also differ depending on location. However, it is the model framework that should be applicable to other reservoirs, and used as a base from which to add. This model is offered as a starting point, a framework on which to refine and make additions, as further information, field data, model testing and analyses of model results, become available.

3.1 Model development tool

Numerous computer software packages are available to assist in the development of system dynamics models. STELLA (Systems Thinking Experimental Learning Laboratory with Animation), version 5.1.1, (High Performance Systems 1994), was used in development of the computer simulation model. It is a tool used for building, exercising and modifying visual representations of mental models (High Performance Systems 1992). The advantages of STELLA are numerous. First, the STELLA software is easy to learn and use. The software allows the user to easily input equations (Ford 1999). Also, STELLA supports a link to a spreadsheet program (i.e., Excel 2000 used in this research). This feature allows the model user to input large data sets with ease. STELLA also enables the user to view model results in tabular or graphical form. Finally, through the development of a user interface, the model inputs can be changed and alternative hypothesis or scenarios can be tested, compared and analyzed.

STELLA models are built using four principal building blocks (objects): stocks, flows, converters and connectors (Figure 7). Stocks (represented as a square) are

accumulations that occur over time. Flows (represented as a broad arrow and circle) in general, represent activities that fill or drain stocks. Flows are inseparable from stocks, you cannot have one without the other (Simonovic et al. 1996). If there is an accumulation, for example, the volume of water in a reservoir, that accumulation has resulted from an inflow (i.e. water into the reservoir). Thus, the volume of water in the reservoir would be represented as a stock, and the water flowing into the reservoir would be represented as a flow. The other two principal building blocks are converters and connectors (Figure 7). Converters (represented as a circle) change inputs into outputs. They are used to capture detail and perform algebraic operations (High Performance Systems 1992). Connectors (represented as an arrow) convey information within the model. They are used to link stocks to converters, stocks to flows, and converters to converters. Connectors are not associated with numerical values or equations, they transmit them.

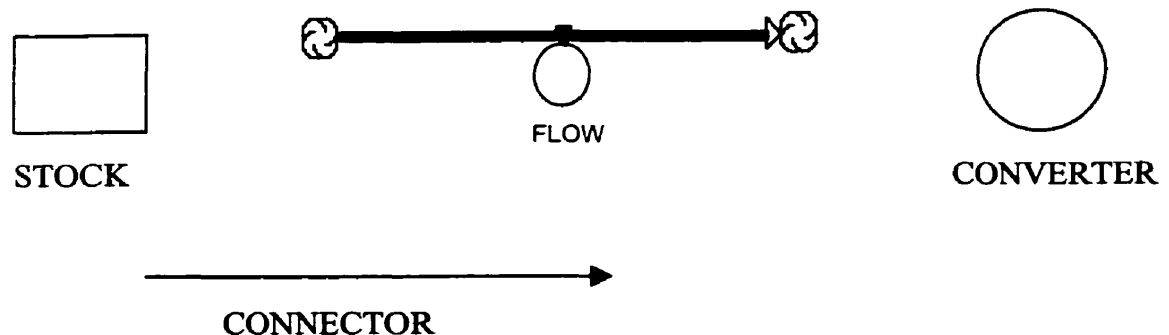


Figure 7. The four principal building blocks of STELLA 5.1.1.

3.2 Modeling process

A phased approach was taken in this research to develop the model framework. The model framework was developed in the following stages:

- (1) identification of important components of the system;

- (2) development of system structure;
- (3) identification and description of system dynamics;
- (4) model refinement/verification; and,
- (5) analyses of results.

3.2.1 Identification of important components

Important components to be included in the model framework were identified using the available literature, and field data from the case study reservoir and other reservoir environments. Chapter 2 provides a review and description of some of the available literature. Figure 4 (included in Chapter 2) provides a conceptual framework of the important components in an aquatic food chain of a reservoir. From these sources, important model components were identified. Since the goal of the model was to test the impact of various alternative hydro operations strategies on fish in a reservoir environment, seasonal water levels and short-term water level fluctuations were identified as key components that model users could manipulate, test and analyze through use of the model.

3.2.2 Development of the system structure

This stage of the modeling process involved relating and inter-connecting the identified components of the reservoir environment, to establish the structure/framework of the model. The goal of this phase was to accurately represent the real-world reservoir environment by arranging the building blocks (i.e., stocks, flows, and converters) within the modeling program STELLA. Development of the model structure was accomplished by identifying connections and inter-relationships between the physical and biological

components of the reservoir system. Literature, expert opinion and relevant field data were used to develop these relationships.

3.2.3 Identification of system dynamics

Identification of reservoir system dynamics involved the development of a database and a set of equations to describe the relationships between inter-related components (represented as stocks, flows, or converters) of the model. Quantitative equations and values used to define the relationships were derived from available literature, previous modeling attempts, data reports and expert opinion. It is important to note that many of the relationships used in model development were not scientifically tested in the Limestone reservoir. Instead, many relationships represent the researchers interpretation of the available literature. Another consideration of this stage of the process was that precise quantitative values and equations for many biological interactions (i.e., predation) often do not exist. Support for the estimation of these relationships was gained from scientific literature, field data, expert opinion and logic.

The development of quantitative relationships between factors over which hydro controls (i.e., reservoir inflows, and reservoir outflows), and the physical characteristics of the reservoir system they influence (i.e., water levels and water velocities) were established using physical reservoir data provided by Manitoba Hydro for the Limestone reservoir. Application of the model framework to another reservoir would require the input of physical data from the reservoir under consideration.

3.2.4 Model refinement/verification

Verification of a model is the determination of whether or not the model performs the way the builder or user expects it to behave (Farmer et al. 1982). To verify this model,

successive simulations were run while adjusting appropriate parameters to produce a model that mimicked the real population of fishes (Taylor 1981). This involved comparing fisheries survey data from the Limestone reservoir to model results, when the historical operating strategies (actual historical data) were used as inputs into the model. Due to the similarities in operation, water chemistry, size and geomorphology between the Limestone and Long Spruce reservoirs, fish populations in the Limestone reservoir are expected to evolve in a similar way as that of the Long Spruce reservoir (Baker 1990). Therefore, fisheries survey data from the Long Spruce reservoir was used to compare with the long-term (i.e., >10 years) model results. When the results of the model reflected the real populations as nearly as possible, experimental simulations were then made to determine the impact of various hydro operations strategies on the fish populations in the Limestone reservoir. In addition, successive simulations were run to test the sensitivity of the model to perturbations of model inputs and parameters. Models refined in a similar fashion include models developed by Taylor (1981), Inskip (1982), and Edwards (1983).

3.2.5 Analyses of the results

The results of the different operating strategies tested by the model were then compared and analyzed. This analysis enables users to identify conditions that may be beneficial or detrimental to fish populations within a hydroelectric reservoir, to discuss and compare model results after each simulation run, and to identify where further research is needed.

3.3 Model development

The following sections describe the development and application of a systems model to the Limestone reservoir. Reservoir discharge data, stage storage curves, and other physical relationships of the Limestone reservoir were used in model development. The structure or framework of the model can be applied to any reservoir for which reservoir morphology data exists.

A fundamental consideration of this research was that mean monthly water levels are not the only important consideration when assessing the impacts of impoundment on fish. Short-term water level fluctuations, caused by hourly fluctuations in discharge, must also be considered important when assessing the impacts of hydro operations on reservoir fish populations. Chapter 2 discussed how both seasonal water levels and the frequency and amplitude of short-term water level fluctuations may have important consequences for fish in the reservoir environment.

In order to consider both the impact of seasonal water levels and short-term water level fluctuations, it was necessary to develop two models. This was because the STELLA software does not allow for the time scale of a model to change during a simulation, and does not allow simulations to run on different time scales within the same model. One model was built using an hourly time increment (named **HYDRAULIC**), run for a one month time period. The other model operates on a monthly time increment (named **FISH**) and was run over a 25 year simulation period. The inputs, outputs and purposes of both models differ, and therefore, each model was discussed separately in the following sections.

3.4 HYDRAULIC model

The model **HYDRAULIC** was developed to accomplish two objectives. The first was to describe how changes in the hourly discharge rate affect water level fluctuations and other physical characteristics of three cross-sections (upper, middle and lower reservoir regions) in the Limestone reservoir. The second purpose was to calculate the maximum fluctuations in water levels and average water velocities that occur over a one month period, and include these calculations as inputs into the **FISH** model.

Manitoba Hydro makes its operational decisions concerning the amount of water to discharge from its reservoirs on an hourly basis. Therefore, hourly discharge rates from the Long Spruce and Limestone G.S. were used as the data inputs for the model. The **HYDRAULIC** model operated on an hourly time step and ran for a one month period (744 hours). The model framework consisted of two levels. The first level included the hourly discharge rates from the Long Spruce and the Limestone reservoir. The second level of the model was comprised of the physical characteristics of the reservoir including water level, cross-sectional area, water velocity, and water depth from the three regions of the Limestone reservoir. The model framework is shown below in Figure 8, and the STELLA diagram is shown in Figure 9.

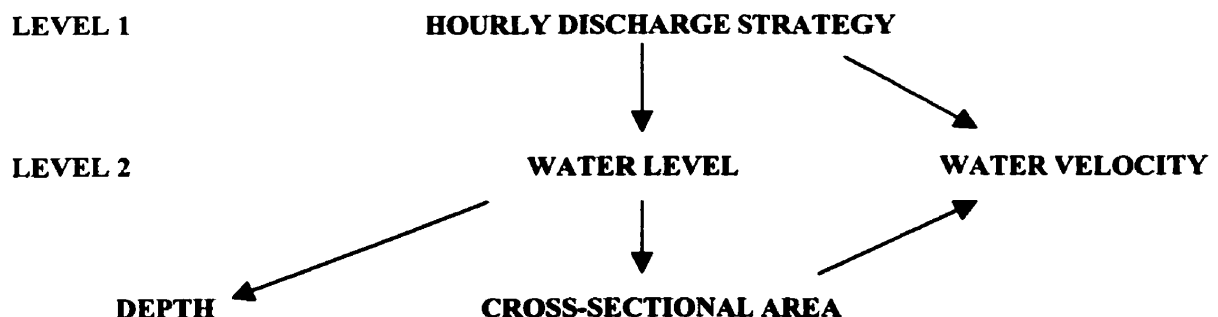


Figure 8. Structural diagram of the **HYDRAULIC** model.

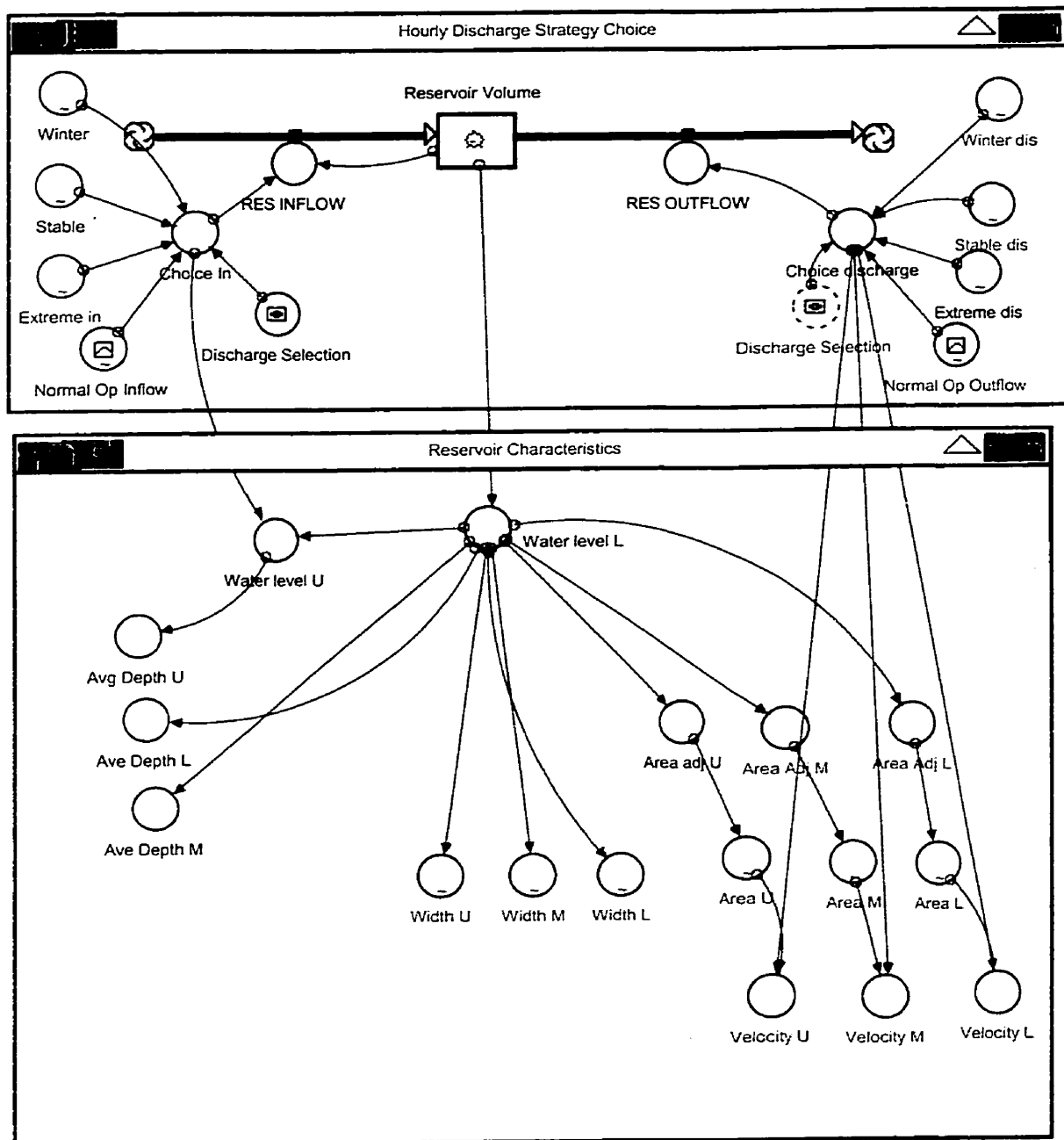


Figure 9. STELLA diagram of the **HYDRAULIC** model.

The **HYDRAULIC** model simplified reality in that it considered the water discharged from the Long Spruce G. S. as the only water inflow. In reality, water inflows from precipitation and inflowing rivers and creeks. However, in relative terms, the importance of these two inflows on an hourly basis to the Limestone reservoir is insignificant when compared to the discharge from the Long Spruce reservoir. Thus, these two inflows were omitted from the model framework.

3.4.1 Model Inputs

Relationships for the model were based on mathematical equations and physical data the Limestone reservoir. Each of the basic inputs used in the model, the basic parameters and their characteristics are described below.

The main model inputs were the discharge rates from the Long Spruce and Limestone generating stations. The discharge rates from the Long Spruce and Limestone reservoirs influence the volume of the reservoir. The volume of water in the reservoir influences the water level, cross-sectional area, and width of each reservoir region. Figure 10 provides the stage storage curve for the Limestone reservoir. The stage storage curve relates the volume of water in the reservoir, to the water level in the reservoir. Figure 11 provides the relationship between the cross-sectional area of the reservoir (Figure 11 shows the cross-section for the upper reservoir region) and water level of the reservoir.

Water level fluctuations in the upper and lower reservoir region were calculated by subtracting the minimum water level from the maximum water level. Water level fluctuations in the middle region were approximated to be:

$$\text{Water fluctuations (middle)} = \frac{1}{2}(\text{Water fluctuations (upper)} + \text{Water fluctuations (lower)}) \dots \dots \dots (1)$$

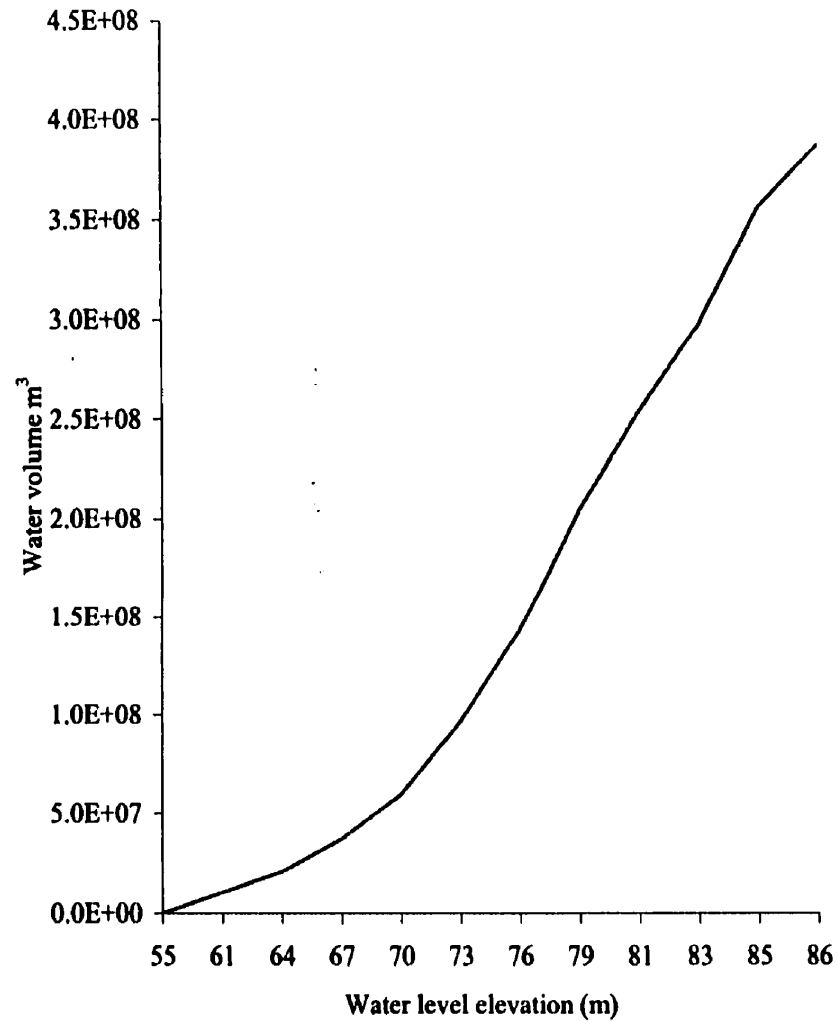


Figure 10. Stage storage curve for the Limestone reservoir (source:Manitoba Hvdro).

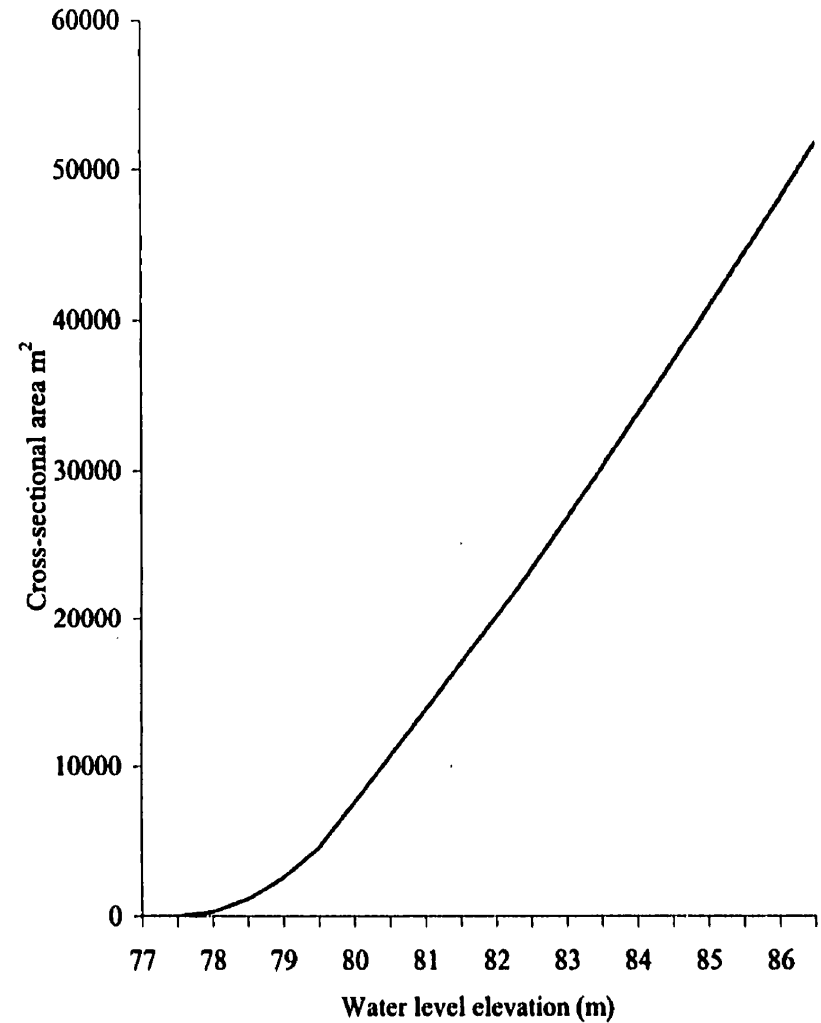


Figure 11. Area of the upper reservoir region vs water level elevation in the upper reservoir region (source: Manitoba Hydro).

Water Velocity in each reservoir region was calculated as a function of discharge from the Limestone reservoir and the cross-sectional area of the reservoir region. For these calculations, the equation provided below was used:

$$\text{Velocity} = \text{Discharge} / \text{Area} \dots\dots\dots (2)$$

3.4.2 Model scenarios

The nature of the **HYDRAULIC** model allows model users to easily generate and test new or alternative discharge strategies. For the purposes of this research, four hourly discharge strategies were analyzed with the **HYDRAULIC** model. The hourly discharge strategies generated and discussed in this thesis were generated based upon their varying impacts that each have upon the physical characteristics of the reservoir environment and fish in a hydroelectric reservoir. The operating strategies were termed: a) historical operating strategy; b) extreme operating strategy; c) stable operating strategy; and d) winter operating strategy. Each discharge strategy is described below.

a) The historical hourly discharge strategy is representative of a typical hourly discharge strategy currently used in the Limestone reservoir. The discharge rate from each generating station was described in Chapter 2 as a pulse release strategy. Pulse releases occur when peak discharge from the generating station corresponds with times of peak power demand, and lower discharge rates occur during periods of relatively low power demand. Figure 12 shows how the hourly rate of discharge from the Limestone reservoir fluctuates over a one month period when the historical short-term operating strategy is used as an input in the **HYDRAULIC** model.

b) The extreme operating strategy represents an extremely variable hourly discharge strategy, in which very high and very low discharge rates occur. Figure 13 shows the

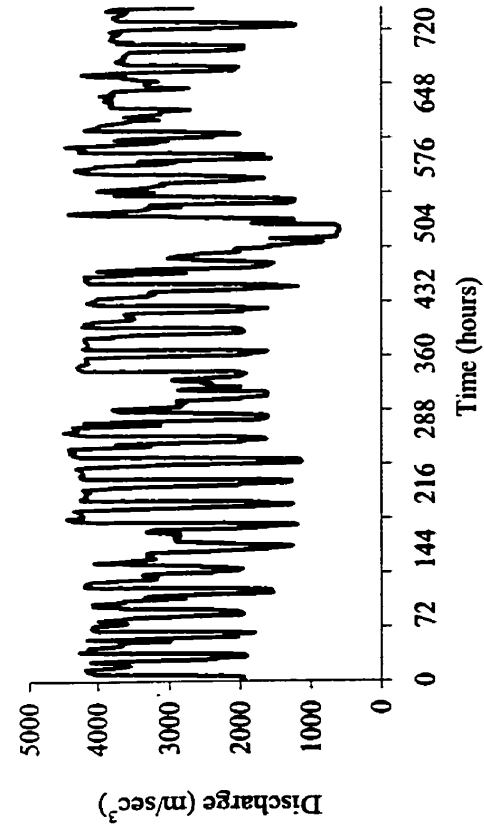


Figure 12. The hourly discharge rate that occurs over one month with the historical operating strategy.

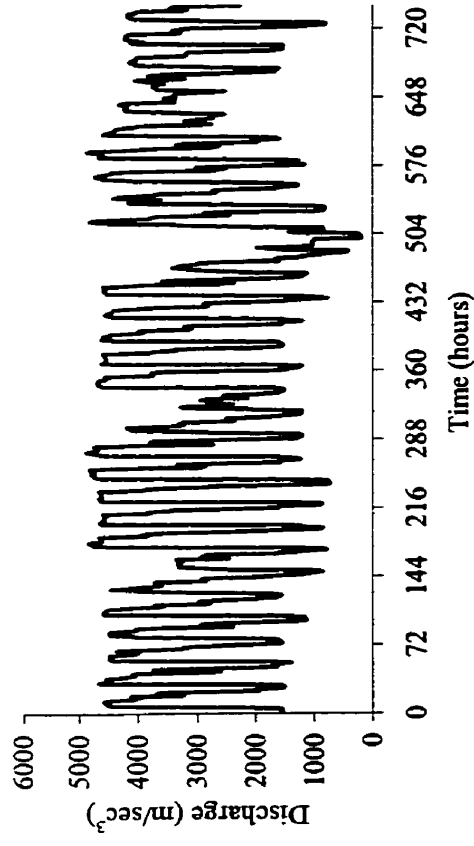


Figure 13. The hourly discharge rate that occurs over one month with the extreme operating strategy.

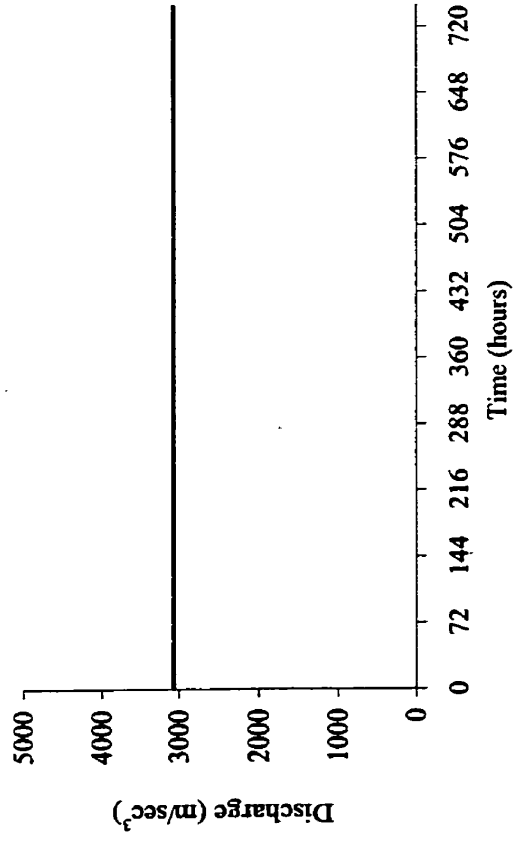


Figure 14. The hourly discharge rate that occurs over one month with the stable operating strategy.

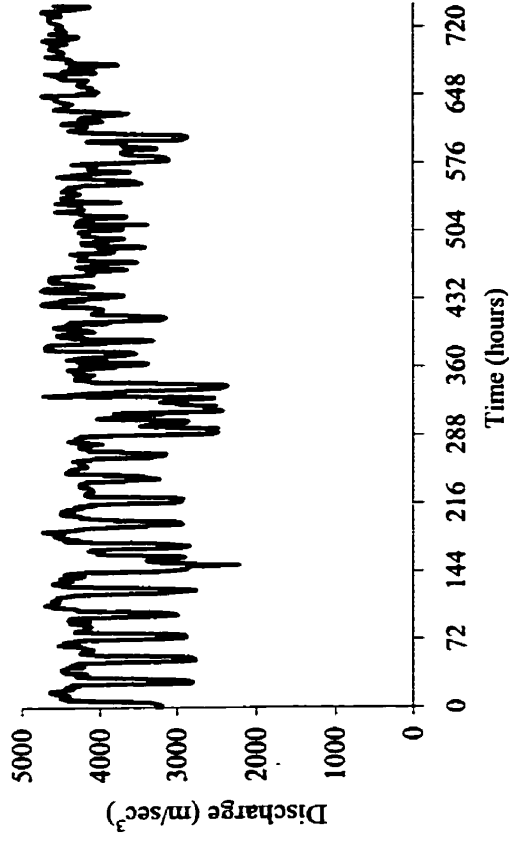


Figure 15. The hourly discharge rate that occurs over one month with the winter operating strategy.

hourly rate of discharge from the Limestone generating station that occurs when the extreme discharge strategy acts as an input into the **HYDRAULIC** model.

c) The stable operating strategy represents a discharge strategy which maintains stable water levels over a one month period in the Limestone reservoir. This was accomplished by setting the discharge rates from the Limestone and Long Spruce generating stations at the same level of $3075 \text{ m}^3/\text{sec}$ as shown in Figure 14.

d) Typically, discharge rates are increased during winter to meet the increase in power demand. The winter operating strategy represents an operating strategy that has been used in the Limestone reservoir during winter, where the rate of discharge remains consistently higher over the one month period. Figure 15 shows the hourly rate of discharge from the Limestone G.S. when the winter operating strategy is inputted into the model.

3.4.3 Model outputs

Outputs from the **HYDRAULIC** model included the short-term fluctuations in water level and average water velocities that occurred within a one month period. These outputs acted as inputs into the **FISH** model and provided support for investigating the long-term impact that alternative hourly discharge rates may have on fish populations in a reservoir.

3.4.4 User interface

A graphical user interface was developed for the purpose of enabling model users to easily manipulate model inputs (i.e., discharge strategies). On the upper mapping layer of STELLA, four “controls” were built in the model two “*graphs*”, one “*slider*” and one “*knob*”. The “*graphs*” enable the model user to manually change the discharge rate from

the Long Spruce and Limestone G.S. The “*knob*” enables the model user to control the initial reservoir volume. By changing the initial volume of water in the reservoir, the impact of alternative hourly discharge strategies can be investigated over a wide range of water levels. The “*slider*” allows the user to choose one of the four discharge strategies described above. The “*slider*” ranges in value from 1 to 4. Moving the slider to (1) selects the historical discharge strategy; (2) selects the extreme discharge strategy; (3) selects the stable discharge strategy; and, (4) selects the winter discharge strategy.

Once a simulation has been completed, model outputs (i.e., water level fluctuations and average water velocities that occur over a one month period) can be viewed in tabular or graphical form on the upper mapping layer of STELLA. In addition, a numeric display built-in to the high-level mapping layer of STELLA allows for easy comparison of results. Established within STELLA are automatic links to Microsoft Excel. They allow model outputs to be viewed and analyzed in either program.

3.5 FISH model

The purpose of the **FISH** model was to predict and evaluate the impacts of short-term fluctuations in discharge, and seasonal water levels on populations of northern pike, lake whitefish, longnose sucker and walleye over a 25 year time period in a hydroelectric reservoir. The outputs from the **FISH** model were numbers of northern pike, lake whitefish, longnose sucker and walleye, large enough to be captured by gillnets, the sampling technique used in fisheries surveys of the Limestone reservoir. In the model, these corresponded to young adult, and mature adult life stages of the fish population. This model operated on a monthly time step and used the outputs from the **HYDRAULIC** model (i.e., water level fluctuations that occurred within a month and

average velocities) and monthly discharge rates from the Limestone reservoir as data inputs.

As previously discussed in Chapter 2, the goal or objective of the model developed in this research differed from traditional fisheries models. Typically, the objective of many traditional fisheries models has been to optimize maximum sustainable yield of a fishery, or, to predict the response or change of population structure and life history parameters in response to exploitation (Beverton Holt 1957, Ricker 1975, Jensen 1981). Frequently, these models do not attempt to deal with factors responsible for influencing the behaviour of the populations (Freeman et al. 1990). In other words, traditional models do not attempt to quantify density independent effects (such as water level fluctuations) on fish populations.

3.5.1 Model structure

The model framework provides an investigator the capability to build upon the existing model and the capability to experiment with life-history parameters of a fish population or alternative hydro discharge strategy. In total, the model framework included four levels. The first level included the monthly discharge rates, and the water level fluctuations calculated with the **HYDRAULIC** model. These were the model inputs. The second level of the model, was comprised of the abiotic components of the reservoir environment. Biological components of the food chain comprised the third level, and the fish species (northern pike, lake whitefish, longnose sucker and walleye) comprised the fourth level. Figure 16 provides the logical framework of the **FISH** model. The four levels that comprised the structure of the model are described in greater detail in the subsequent section.

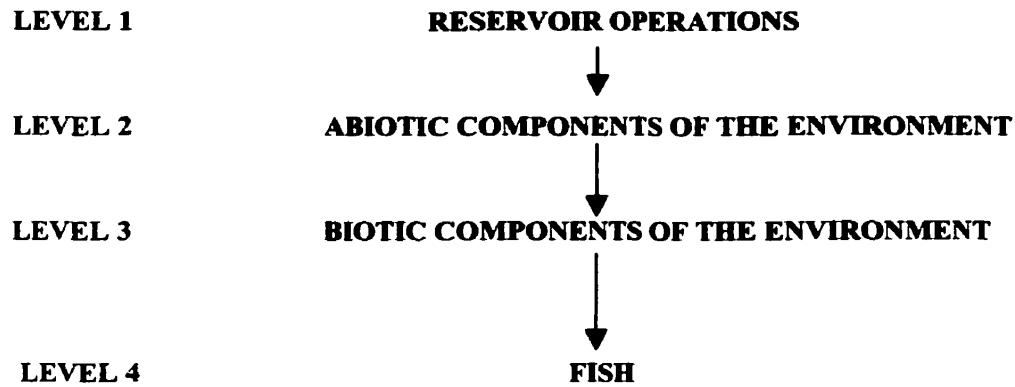


Figure 16. Structural diagram of the **FISH** model.

3.5.1.1 Reservoir operations (Level 1)

Level 1 of the **FISH** model was comprised of the results of the short-term discharge strategies tested by the **HYDRAULIC** model, and the monthly water volume discharged from the Limestone and the Long Spruce reservoirs. For the purposes of this thesis, two monthly discharge strategies, (named historical and spring flood) were generated to investigate, in combination with an hourly discharge strategy, the impacts of alternative monthly water level strategies and hourly discharge strategies on fish in the Limestone reservoir. The monthly water level strategies are described below.

(a) Historical monthly operating strategy

The historical monthly operating strategy represents the actual water levels that have occurred in the Limestone reservoir since 1989. Figure 17 provides the water levels that have occurred in the Limestone reservoir from 1989 to 1998. Figure 17 shows that since 1993, mean monthly water levels in the Limestone reservoir have remained relatively stable. However, it must be remembered that water levels are fluctuating in the reservoir, but on an hourly basis, but these fluctuations are not observable when looking at mean monthly water levels. These short-term fluctuations are included in this model, by

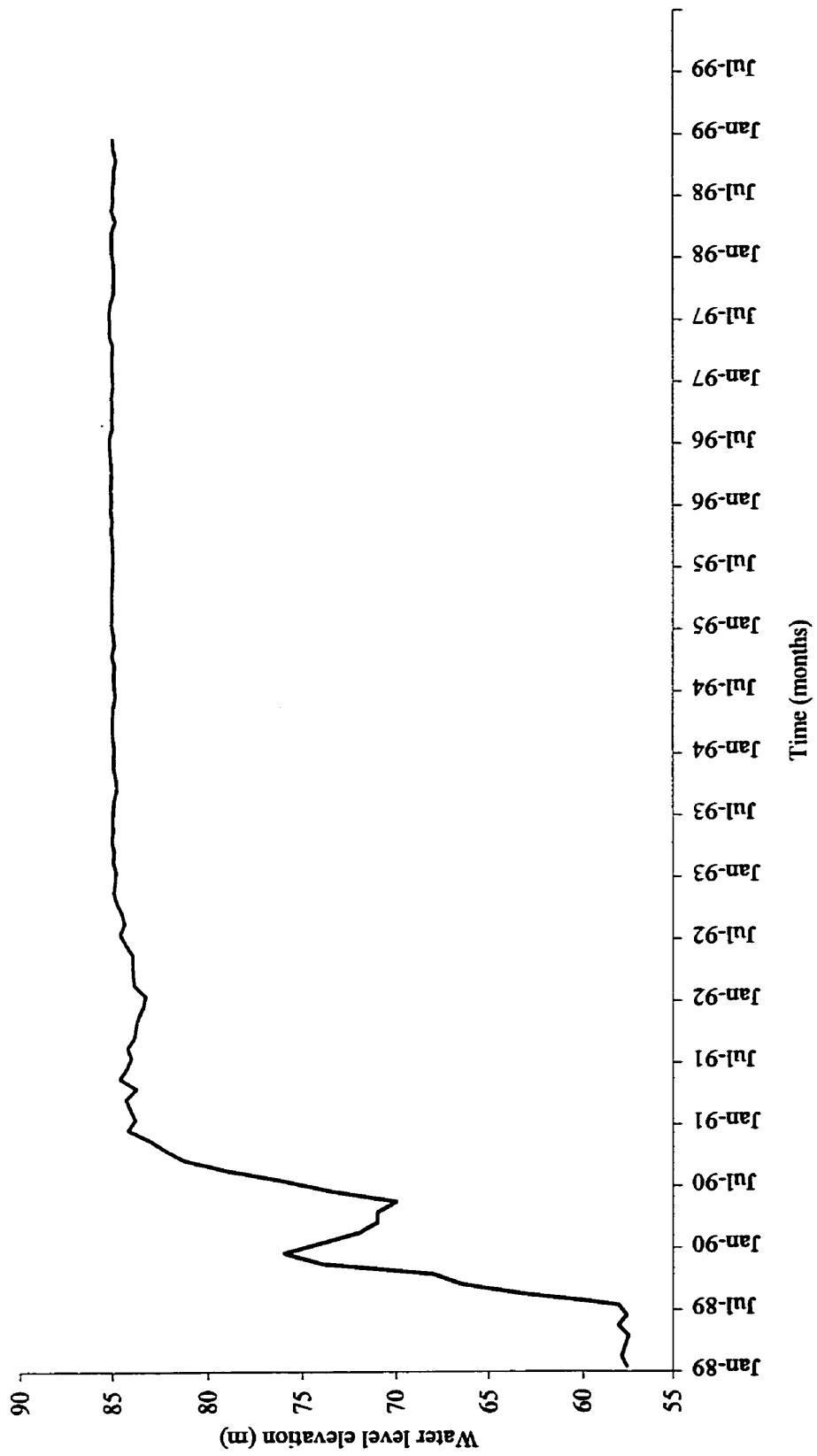


Figure 17. Historical water levels in the Limestone reservoir 1989 - 1999.
(source: Manitoba Hydro).

including the results of the **HYDRAULIC** model. Therefore, model users can choose a monthly water level strategy, in combination with a short-term discharge strategy.

(b) Spring flood monthly operating strategy

The second seasonal discharge strategy investigated with the **FISH** model is the spring flood seasonal operating strategy. This strategy was discussed in Chapter 2 and shown graphically in Figure 5 (Chapter 1). Groen and Schroeder (1978) and Plosky (1986) suggest that this seasonal water level management strategy may benefit fish in hydroelectric reservoirs.

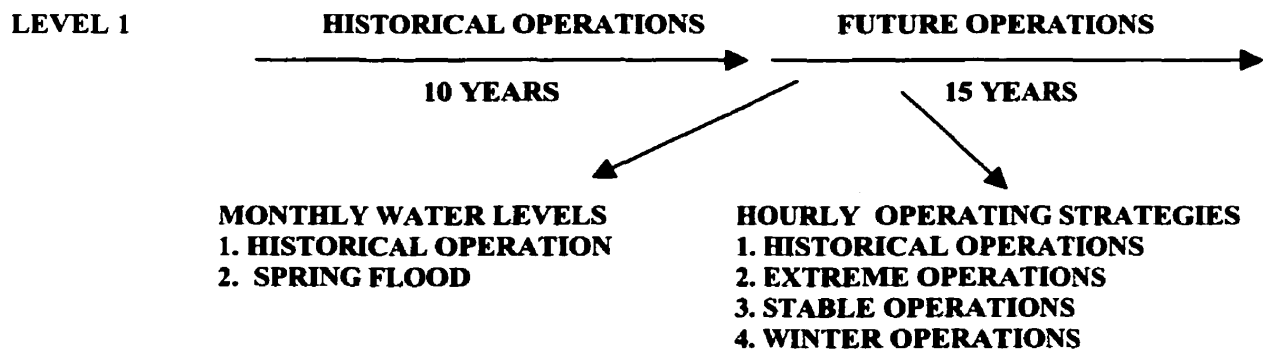


Figure 18. Structural diagram of Level 1 of the **FISH** model.

Level 1 of the model was separated into two time periods: historical operations and future operations (Figure 18). This was done to account for the past operations of the Limestone reservoir, which has been operated for 10 years. Therefore, the model uses historical data for the first 10 years of the simulation, and uses a combination of monthly water level strategy, and short-term operating strategy, chosen by the model user, for the remaining 15 years. This thesis presents the results and analysis of two alternative monthly discharge strategies (historical and spring flood) and the four alternative hourly discharge strategies (historical, extreme, stable and winter), shown in Table 1, on the four fish species included in the model.

3.5.1.2 Abiotic features of the reservoir environment (Level 2)

Level 2 was comprised of the abiotic features of the reservoir environment including: depth; flooded area; width of the reservoir; nutrients; total suspended solids; and chlorophyll *a*. The structure of Level 2 is shown in Figure 19. The relationships used in the model that related cross-sectional area, width, and average depth of each reservoir region to water level in the Limestone reservoir were developed using the same graphical relationship used in Level 2 of the **HYDRAULIC** model. The only relationship used that was not previously discussed in development of the **HYDRAULIC** model, was flooded area of the Limestone reservoir. Figure 20 shows the relationships between the flooded area and volume of water in the Limestone reservoir.

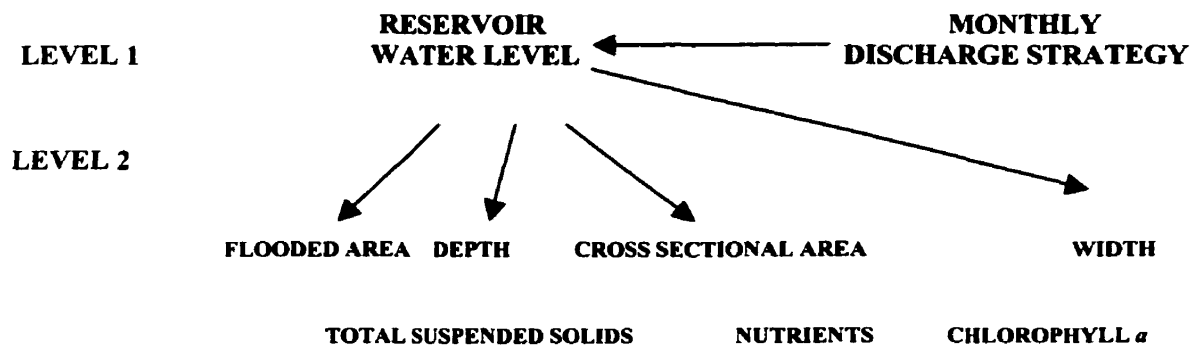


Figure 19. Structural diagram of Level 2 of the **FISH** model.

At the outset of the research it was hoped that relationships could be developed between Level 1 of the model and measures of total suspended solids, nutrients, or chlorophyll *a* values from the Limestone reservoir. Although total suspended solids, nutrients and chlorophyll *a* have been discussed in the scientific literature as being correlated with discharge rate, or flooded area for example, (see Chapter 2), no correlation could be established with water quality data from the Limestone reservoir. In the Limestone and Long spruce reservoirs, concentrations of total suspended solids,

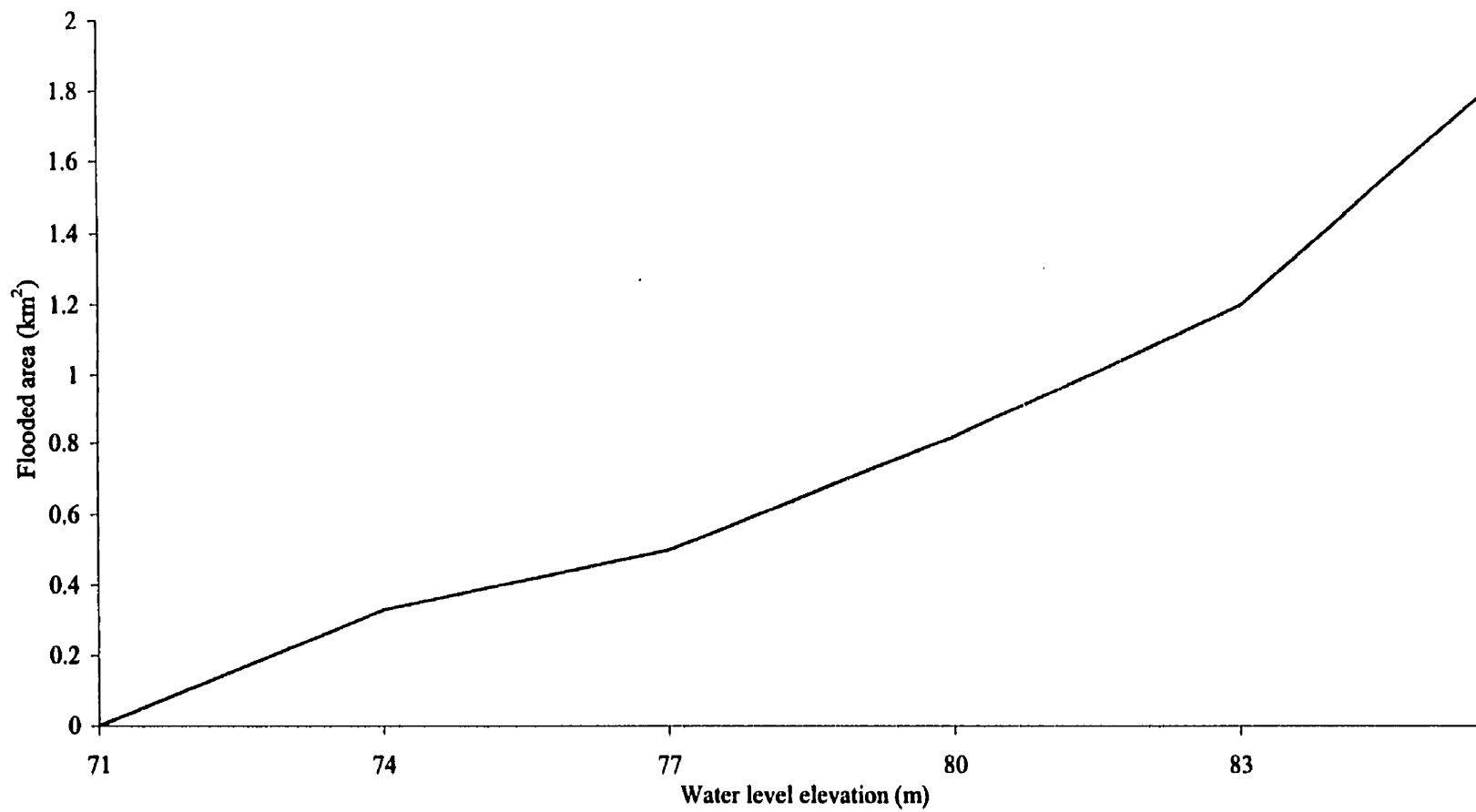


Figure 20. Flooded land area vs water level elevation in the Limestone reservoir.
(source: Manitoba Hydro).

nutrients and chlorophyll *a* have remained relatively unchanged despite the changes that have occurred to the flow regime and physical characteristics of the reservoir following impoundment (Zrum and Kennedy 2000).

Although these water quality parameters have not changed since development of the Limestone reservoir, they are important considerations for fish and other aquatic life in reservoir ecosystems. For future applications, these water quality parameters were included in the model framework. With the exception of total suspended solids, these parameters were not incorporated into any relationships which influence the fish populations.

3.5.1.3 Biotic components of the reservoir ecosystem (Level 3)

Level 3 was comprised of biotic features of the reservoir environment identified as important components of fish diet. These included populations of forage fish, zooplankton, smelt, and invertebrates. In the initial stage of the research it was hoped that relationships could be established between abiotic features of the reservoir (Level 2) and the biotic components of the reservoir (Level 3). However, no relationships between these levels were found in the data from the Limestone reservoir. This was because: a) no data has been collected on zooplankton or forage fish abundance in the Limestone reservoir, and, b) the data that has been collected on invertebrates and smelt could not be related to any component of Level 2.

Monitoring forage fish, zooplankton, smelt or invertebrate populations in a hydroelectric reservoir is difficult due to the number of different species and numbers of individuals which comprise each population. Accurately estimating the total number of individuals in a reservoir is challenging due to the amount of field data required, and due

to errors associated providing a population estimate. Therefore, deriving relationships for a model based on total numbers of forage fish, zooplankton, smelt and invertebrate in a hydroelectric reservoir is problematic.

When monitoring invertebrate, forage fish, smelt and zooplankton populations following impoundment, it may be more valuable to compare abundances from field data collected prior to and following impoundment. In this way, a relative comparison of abundances could be provided, rather than an estimate of the total number of individuals in a population. A post-impoundment monitoring program should be established that could provide a comparison of numbers from year to year. These data could provide an estimate of the magnitude of change that may have occurred in the reservoir following impoundment.

Developing relative abundance estimates to include in the model framework for zooplankton and forage fish was difficult due to the lack of data from the Limestone reservoir. Machniak (1975b), Therien (1981), Petts (1984), and Kimmel and Groeger (1986) suggest that in many reservoirs correlations exist between levels of chlorophyll *a* and zooplankton, nutrients and zooplankton, and zooplankton and forage fish, for example have been established. As previously discussed, in the Limestone reservoir, measures of chlorophyll *a* and nutrients have remained relatively unchanged following impoundment. If a correlation existed between nutrient levels, zooplankton and forage fish abundance, as the literature suggests, then we would assume that zooplankton and forage fish populations have also remained relatively unchanged following impoundment. For the model framework, the relationships developed for the relative abundance of zooplankton and forage fish were assumed to remain constant throughout the simulation.

Although no data exist on zooplankton or forage fish abundance in the Limestone reservoir, data were available for smelt and invertebrates. Stomach content analyses from fish captured during fisheries surveys in the Limestone reservoir suggest that smelt may be increasing in the reservoir. As discussed in Chapter 2, the first smelt specimen was found in the Limestone reservoir in 1996. By 1999, smelt were found in 70% of pike stomachs and 52% of walleye stomachs that contained food items (Bretecher and MacDonell 2000). The relationship for smelt abundance on a relative scale is shown in Figure 21. The relationship assumes that the smelt population begins to increase in the reservoir eight years after impoundment, reaches a peak 15 years after impoundment and remains constant for the remainder of the simulation. Future data collection may provide additional information for this relationship.

Invertebrate data from the Limestone reservoir suggests that initially invertebrate populations were reduced following flooding, but as early as 1999 may have become re-established to pre-impoundment levels (Kennedy and Zrum 2000). The relationship is shown in Figure 22 which shows an initial 10% decrease in the number of invertebrates, and the subsequent stabilization to pre-impoundment levels (Baker and Schneider-Vierra 1993). Further data collection may provide data necessary to change or manipulate this relationship.

It should be noted that relationships developed with the relative scale which remain unchanged throughout the simulation, (i.e., zooplankton and forage fish) were included in the model framework for future applicability of the model, and to allow model users to test model sensitivity to changes in their abundance. If future data collection from the

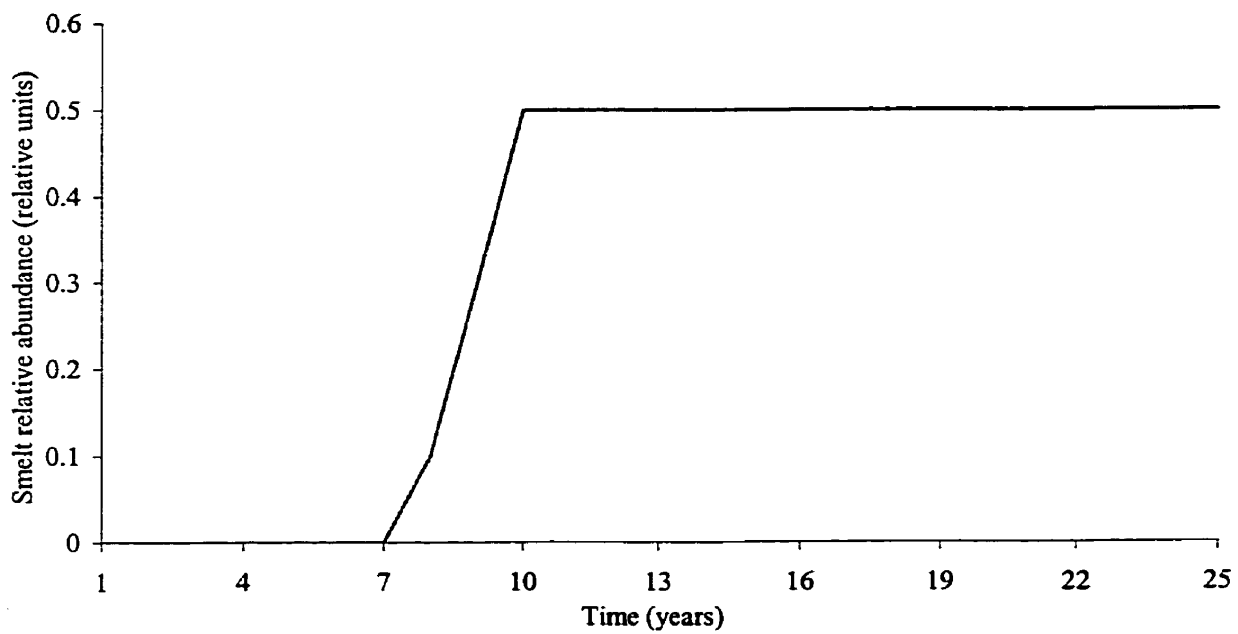


Figure 21. Relative abundance of smelt over time in the Limestone reservoir.

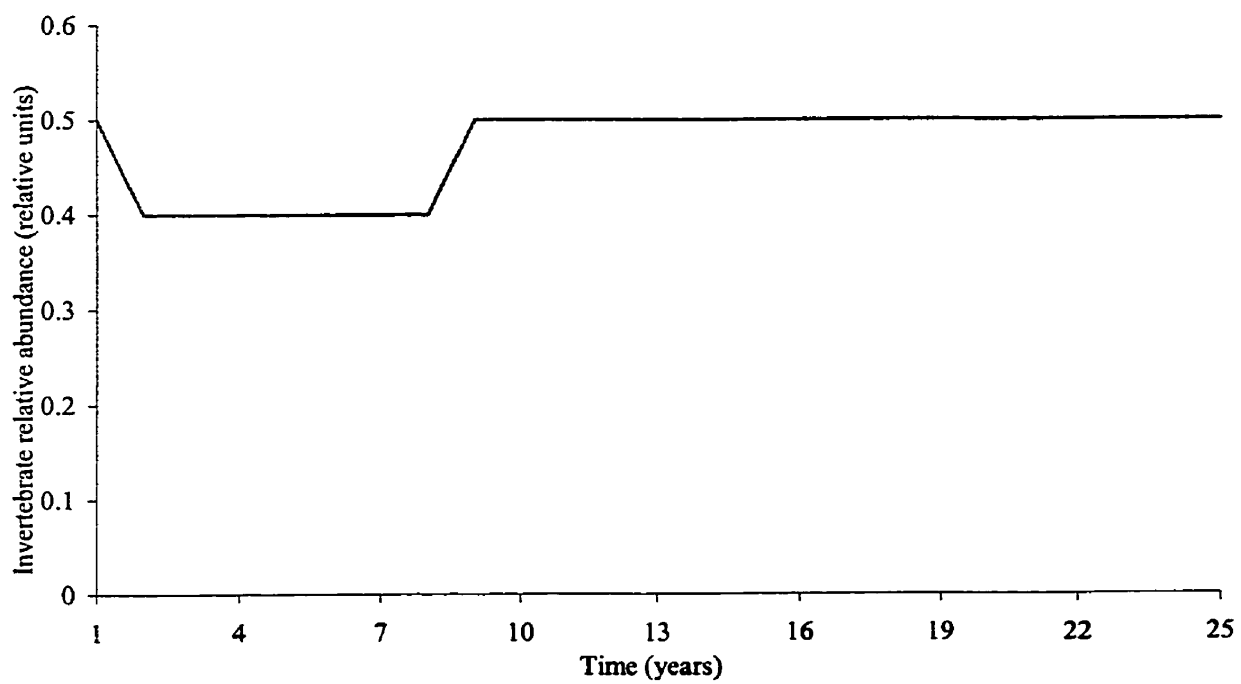


Figure 22. Relative abundance of invertebrates over time in the Limestone reservoir.

Limestone reservoir suggests an increase or decrease in the relative abundance, then the relationship can be adjusted accordingly.

3.5.1.4 Fish (Level 4)

The framework of the entire **FISH** model is provided in Figure 23. Level 4 was comprised of the four fish species included in the model: northern pike, longnose sucker, lake whitefish and walleye.

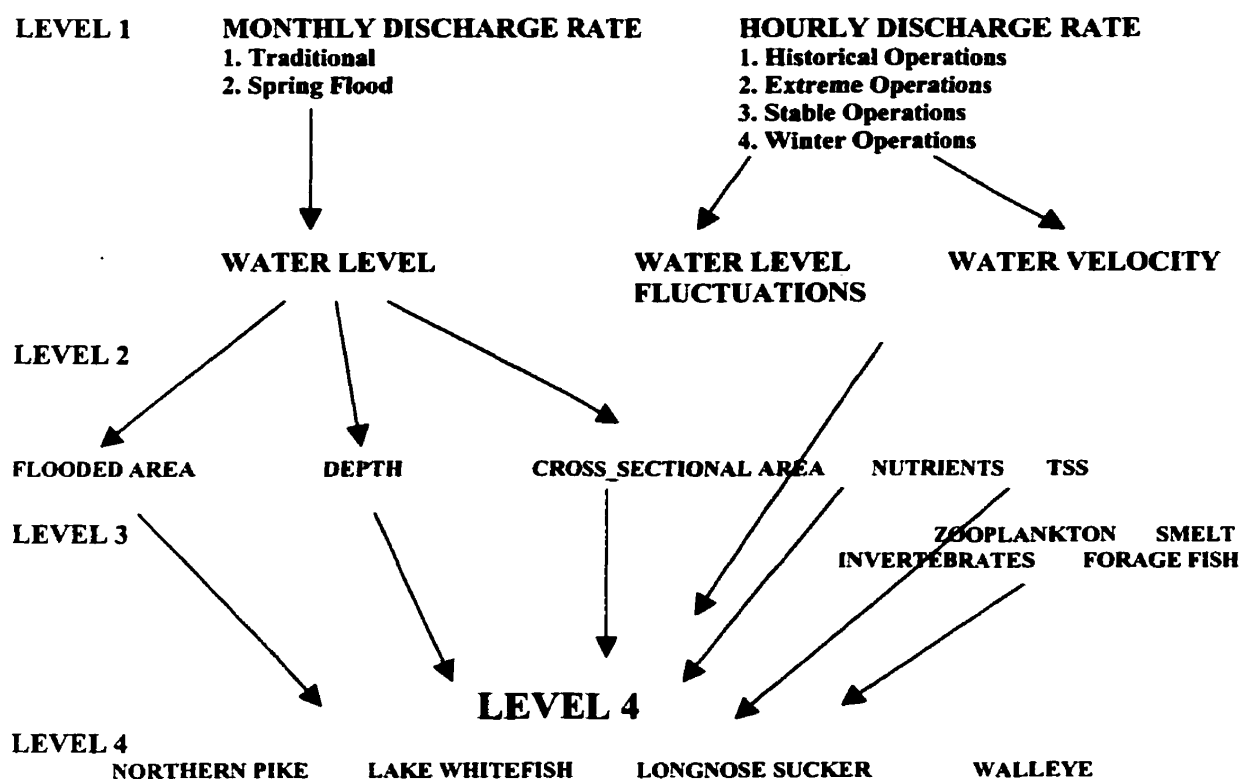


Figure 23. Framework of the **FISH** model.

In fishery systems, basic population parameters such as mortality and predation are not necessarily equal for all age classes (Ricker 1975, Taylor 1981). In addition, the impact that reservoir development and water level fluctuations may have on the fish may also differ depending on the age of the fish. Therefore, to account for the different impacts of reservoir development that occurs throughout a fish's life, the model framework was developed with seven life phases for each fish species. The phases

included egg, larval, juvenile, one to two year old, young adult, mature adult and older mature adult. This age structure was similar to other systems models developed by Hannon and Ruth (1997) for gizzard shad, and a model developed for sockeye salmon (Ford 1999). This type of age structure is valuable for systems where information on growth is limited and difficult to predict over time (Ford 1999). Growth is discussed in section (3.6).

In order to account for the different spawning conditions that may exist in a reservoir, the model framework was developed with separate sectors for the upper, middle and lower reservoir regions. Each of these sectors contained accumulations of fish eggs, and larvae, for each fish species. These accumulations were affected by the physical conditions of each reservoir region. Including different regions in the model framework provides the model user the capability to investigate the sensitivity of the model to fish spawning in a certain region of the reservoir, and provides the capability of incorporating site specific spawning information. For example, if the model was applied to a reservoir with separate basins, the model could account for the different spawning conditions that may exist between basins. Once fish reach the juvenile life cycle stage they are grouped into a single accumulation, representative of the entire reservoir. As previously discussed, outputs for the model were the numbers of individuals comprising the last three life stages of each fish species (ages may differ depending on age at maturity and life-expectancy of each species).

Weather may be a critical factor affecting the survival of the early life-stages of many fish species (Regier et al. 1969). In nature, fluctuating water temperatures for example, may cause a high mortality of eggs. Hansen et al. (1998) modeled the recruitment

variation of walleyes in Escanaba Lake, Wisconsin. Included in this model was a random variable for water temperature fluctuation during the spawning period. The model developed by this research did not include a random variable for weather in the framework. The goal of this model was to predict general trends in fish abundance following reservoir development. Inclusion of a random weather variable may mask these trends. Also, weather is impossible to predict or control, especially over a 25 year time period, and was therefore not included in the model framework.

Population estimates for the fish species included in the model prior to impoundment of the Limestone reservoir were not completed. Baker (1990) reported a population estimate of the longnose sucker population from the Limestone reservoir in 1989. Based on a Schnabel population estimate, the longnose sucker population was found to range between 36,824 and 86,183. Fisheries survey data from this study suggested that longnose sucker comprised 91% of the total catch, and that the abundance of other fish species in the reservoir were several orders of magnitude less (1.4% for lake whitefish, 1.0% for northern pike and 0% for walleye). The initial population estimate for longnose sucker used in the model was 82,000. Relative to this estimate, 7,850 was used for northern pike, 8,350 for lake whitefish and 1,350 for walleye. Based on the composition of the catch in Baker (1990), these estimates may be considered high, however, due to the fishing sites used in the survey, it is possible that longnose sucker were over-represented in the catch.

Northern pike

The effects of reservoir development on northern pike have been documented on numerous reservoirs around the world. As discussed in Chapter 2, following river

impoundment, northern pike typically increase in abundance, followed by a subsequent decrease. This trend has been noted widely throughout the literature by Hassler (1969), Cooper (1971), Benson (1980), Bodaly and Lesack (1984), Kupchinskaya (1985), Deslandes et al. (1994). Understanding the factors that influence this trend in would help managers effectively predict how northern pike populations may be affected by reservoir development. The age structure of the northern pike sector of the model is provided in Figure 24.

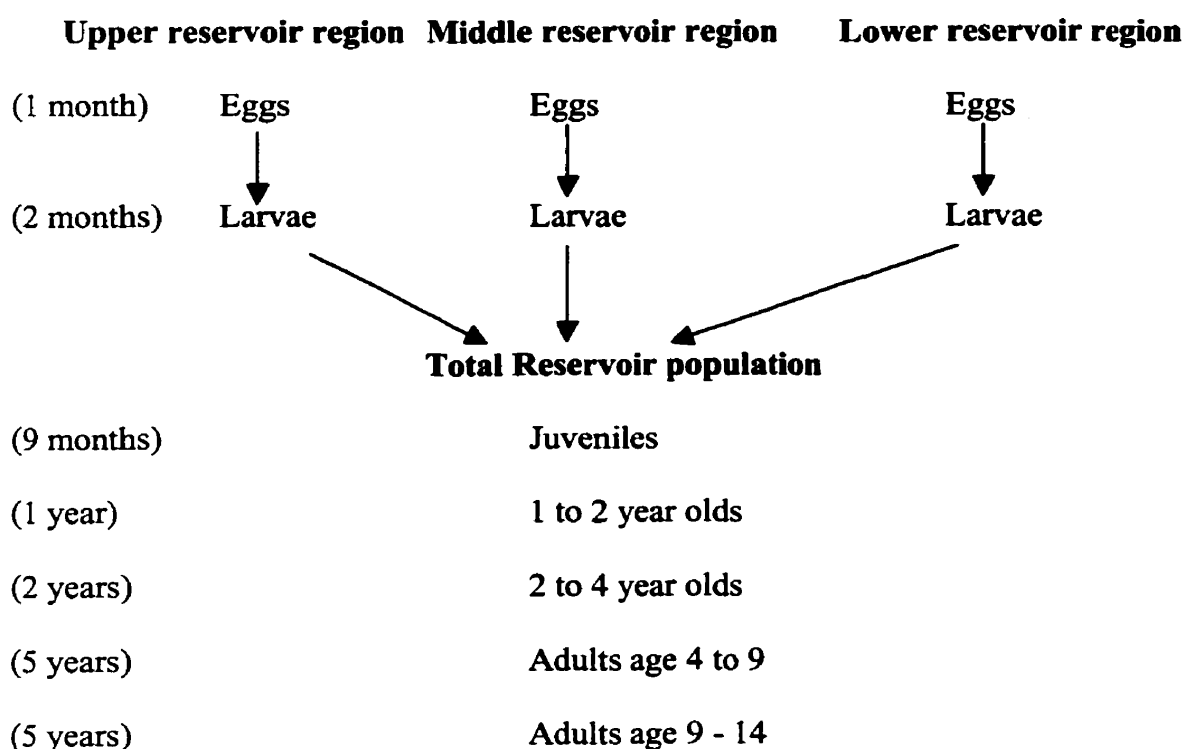


Figure 24. The structure of the northern pike sector of the **FISH** model.

Northern pike are spring spawners. Spawning generally occurs over flooded vegetation in shallow water (Clark 1950, Scott and Crossman 1973, Inskip 1982) and time of spawning generally depends upon water temperature (McPhail and Lindsey 1970, Scott and Crossman 1973, Inskip 1982). Since water temperatures appropriate for spawning generally occur during May in the Limestone reservoir, the model assumes that

northern pike spawn during the fifth month of each simulation year. The number of eggs laid by northern pike each year are influenced by three density independent parameters. These parameters are fixed and assumed to remain constant over the entire simulation period. First, it is assumed that half the spawning population is female. Second, the model assumes that 60% of the eggs are fertilized. This percentage is based upon estimates made by numerous authors included in Machniak (1975a), whose estimates ranged between 0.5 and 0.9. Finally, since fecundity of fish is generally based upon weight of the fish, older northern pike (age 9 to 14) are assumed to lay 32,000 eggs, and younger northern pike (age 4 to 9) are assumed to lay 22,000 eggs. These numbers are based upon average estimates included in Carbine (1942), Scott and Crossman (1973) and Inskip (1982).

The above model inputs are user-supplied coefficients. These user-supplied coefficients are also included in the model framework for each fish species. These coefficients can be determined from field data, if data exists, or estimated using available literature. In other instances, coefficients can be estimated from knowledge of the population and then adjusted where needed when fine-tuning the simulation. The values provided above were used during the simulations explained by this thesis. Future model users may investigate the results of changing these inputs.

The presence of flooded vegetation may be the most important factor affecting the spawning success of northern pike in hydroelectric reservoirs. Strong year-classes of northern pike often occur as a newly created reservoir fills, and when exceptionally high spring water levels flood previously unflooded terrestrial vegetation. The abundance of flooded vegetation after the initial development of a reservoir has been correlated with

highly successful year classes (Holcik 1968, Hassler 1970, Cooper 1971, Gorodnichii 1971, June 1976, Groen and Schroeder 1978, Nelson 1978, Bodaly and Lesack 1984, Strange et al. 1991). Newly flooded terrestrial vegetation is thought to provide northern pike with high quality substrate which may result in increased egg survival, by reducing egg predation. The relationship used in the model relating flooded area to egg survival is shown in Figure 25. This relationship assumes that the amount of newly flooded area positively correlates with an increase in northern pike egg survival.

Holcik (1968), Benson (1980) and Bodaly and Lesack (1984) discuss that after a period of time being submerged, that the character of the vegetation changes and no longer offers valuable nursery habitat which increases egg survival. The length of time required for vegetation to degrade has been estimated at approximately two to four years (Inskip 1982, Bodaly and Lesack 1984, Strange et al. 1991). The model calculates the amount of flooded area available for northern pike spawning by subtracting the amount of flooded area at the end of the fall season (October), from the amount of flooded area in the spring (May). The model assumes that the flooded vegetation degrades two years after initial flooding. (This calculation is termed the flooded area index, and is used in the relationships shown in Figure 25 and 28).

It has been suggested that pike production in reservoirs may be affected by reservoir operation. Holcik (1968), Machniak (1975a), Benson (1980) and Gaboury and Patalas (1984) discuss that rising and maintained high water levels are optimal for northern pike reproduction. Fluctuating or low water levels during egg incubation and nursery periods have been correlated with poor northern pike spawning success (Johnson 1957, Wajdowicz 1964, June 1970, Hassler 1970, Walburg et al. 1971, Cooper 1971, Il'ina and

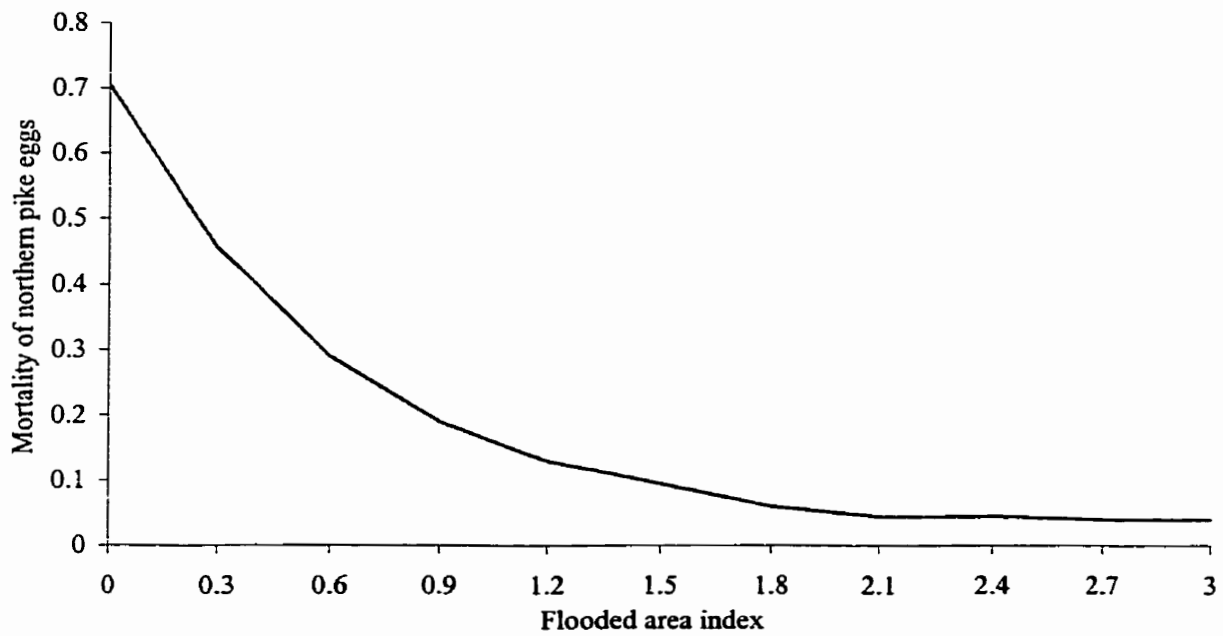


Figure 25. Relationship between northern pike egg mortality and the flooded area index.

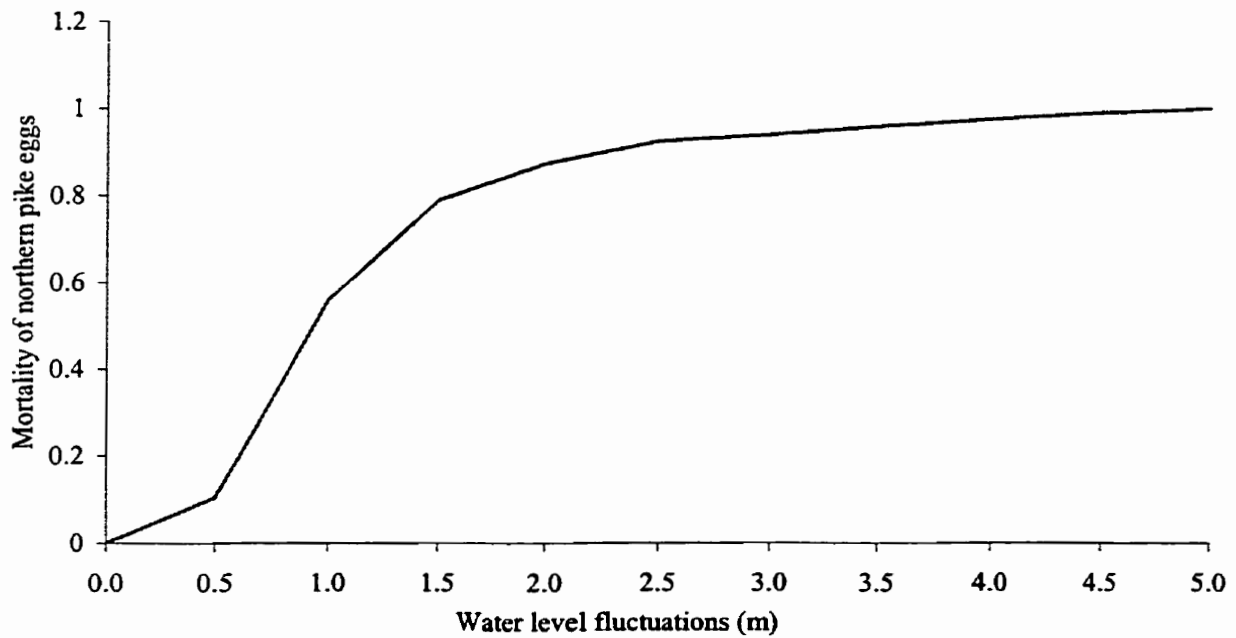


Figure 26. Relationship between mortality of northern pike eggs and water level fluctuations.

Gordeev 1970, 1972, Nelson 1978, Inskip 1982, Casselman and Lewis 1996). Despite the correlation implied by many authors between water level fluctuations and year classes of pike, few authors have provided estimates on the amplitude of water level fluctuations and the magnitude of impact those fluctuations may have on northern pike egg mortality. Johnson (1957) ranked northern pike year class strength in Ball Club Lake, Minnesota, and concluded that high spring water levels and a small decline in water level during egg incubation represented good conditions for northern pike. During his seven year study, he found that water level fluctuations of 0.5 m corresponded to the lowest recruitment of northern pike. Masse et al. (1992) on Riviere aux Pins (Quebec) found that a controlled water level conditions and high spring water levels may have resulted in a much higher egg survival rate from 0.037% to 0.399%. Clark (1950) suggested that pike may spawn in less than 0.5 m of water and thus water level fluctuations over 0.5 m may have adverse impacts on pike spawning success. Casselman and Lewis (1996) considered gradually increasing water levels prior to spawning, stable water levels until larvae move from spawning grounds, then gradually decreasing water levels, as optimal water level management for northern pike. Figure 26 shows the relationship used in the model which relates fluctuating water levels to the proportion of northern pike egg mortality. This relationship assumes that as water level fluctuations increase, the mortality of northern pike eggs also increases.

Northern pike larvae may also be adversely affected by fluctuating water levels. Machniak (1975a), Inskip (1982) and Casselman and Lewis (1996) suggest that newly hatched northern pike larvae become inactive after an initial burst of activity and may be stranded by fluctuating water levels. Inskip (1982) developed a habitat suitability index

to quantify the impact that water level fluctuations may have on northern pike larvae. The relationship used in the model is based on Inskip (1982) and assumed that as water level fluctuations increased, the mortality of northern pike larvae also increased (Figure 27).

Larval northern pike are thought to be affected by two factors: predation and food availability (Strange et al. 1991). Flooded vegetation may influence the predation rate of northern pike larvae by providing a favourable nursery area to escape predation (Frost and Kipling 1967, Inskip 1982, Holland and Huston 1984, Strange et al. 1991). Carbine (1938) found that yellow perch, various invertebrates and water birds are predators on larval northern pike. Although many of these predators are not included in the model, the relationship used in the model framework assumes that the mortality rate of northern pike larvae correlates to the flooded area index (Figure 28). Food availability has been found to be a major influence on the survival of all fish species at the larval lifestage, including northern pike (May 1974, Morrow et al. 1997). In the initial stages of larval development, northern pike larvae feed predominantly on zooplankton (Frost 1954, Lawler 1965, Diana 1979, Morrow et al. 1997). Hassler (1970) found that after hatching, food supply was more important to larval pike survival than other physical factors such as predation. Inskip (1982) and Morrow et al. (1997) identified the availability of zooplankton immediately after hatching as a major influence on the mortality rate of northern pike larvae.

A mortality factor was built into the model which assumes a decreased larval northern pike mortality rate with a higher relative abundance of zooplankton. Figure 29 provides the relationship used as an input into the model. The shape of the graph suggests that a

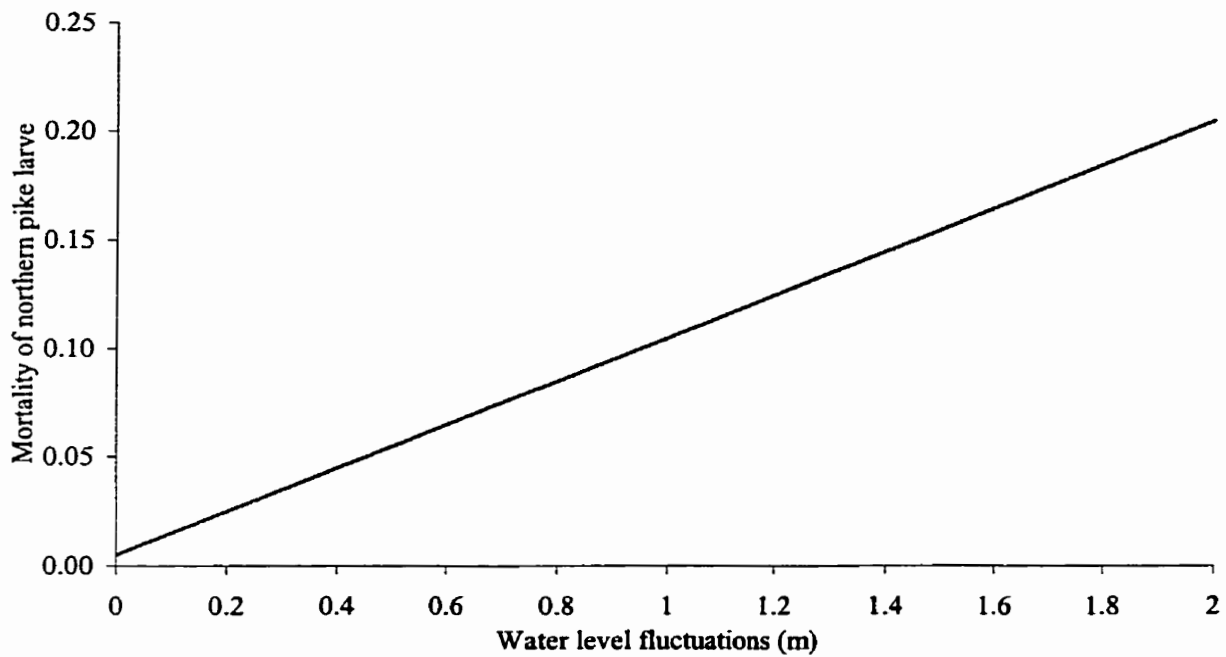


Figure 27. Relationship between mortality of northern pike larvae and water level fluctuations.

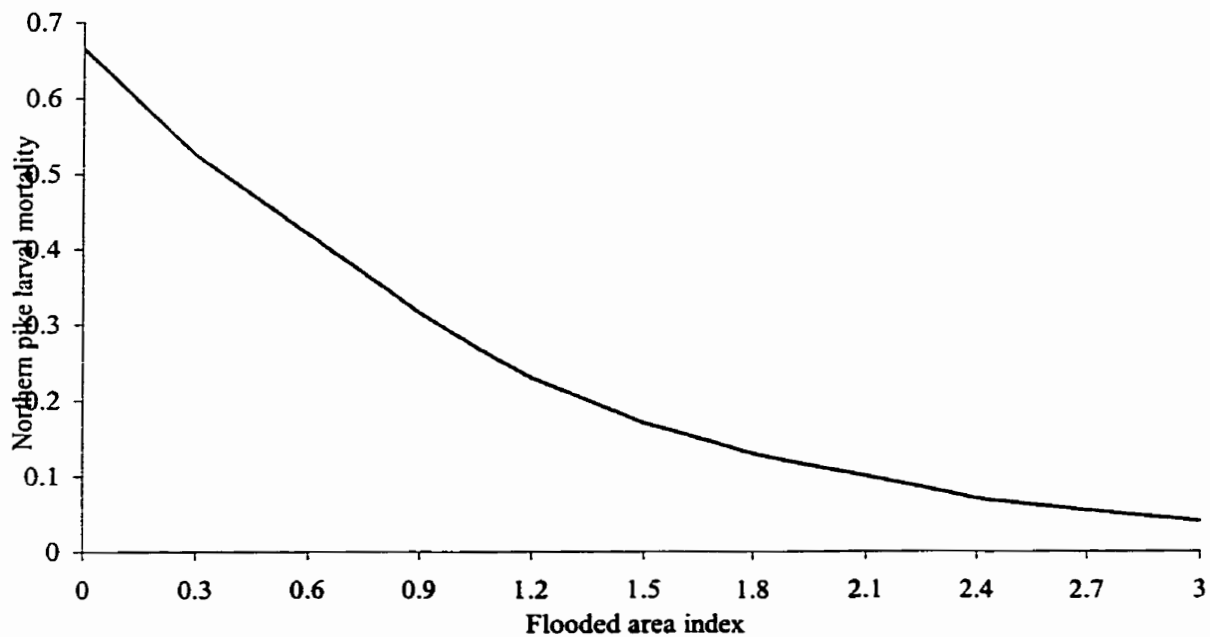


Figure 28. Relationship between northern pike larval mortality and the flooded area index.

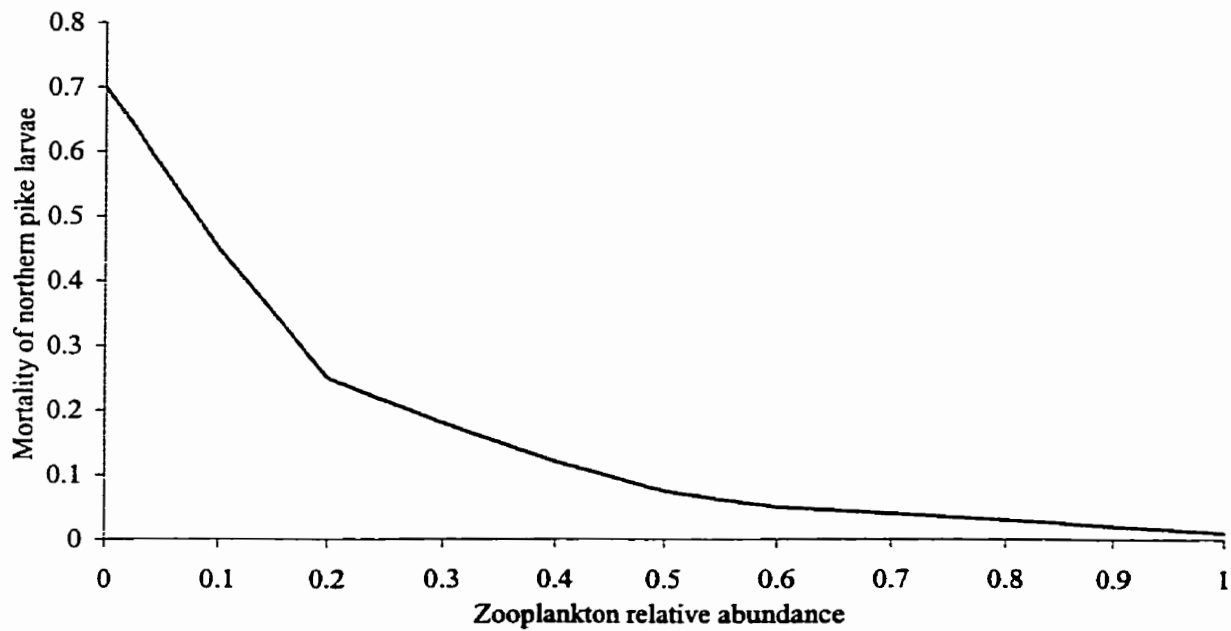


Figure 29. Relationship between the mortality of northern pike larvae and zooplankton relative abundance.

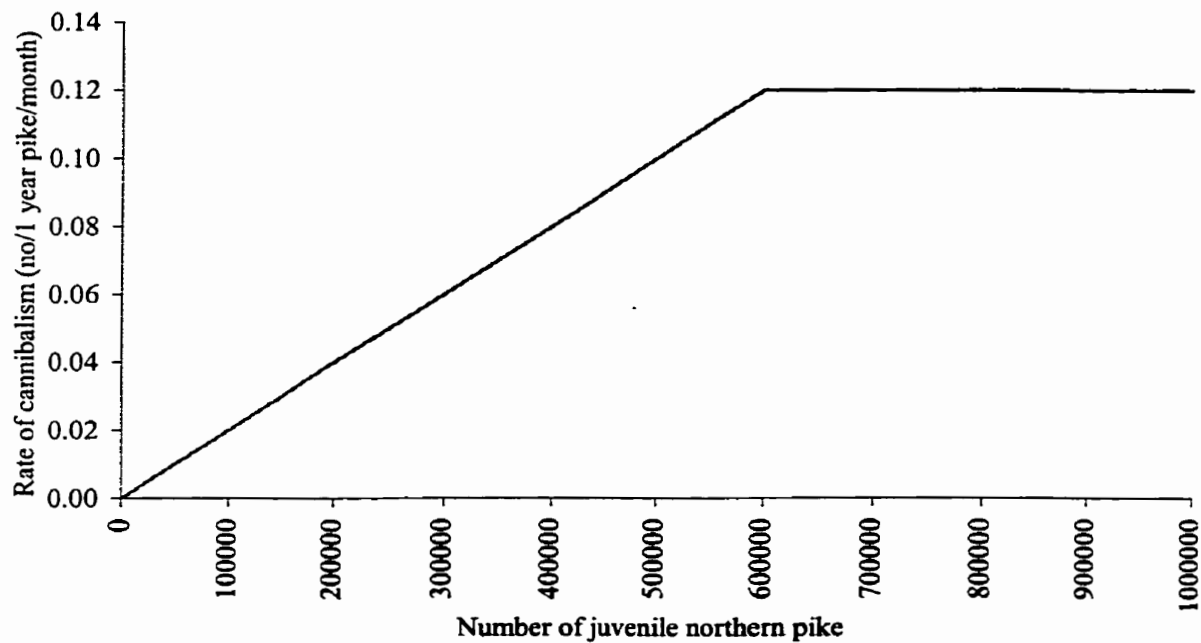


Figure 30. Relationship between the juvenile predation rate per month and the number of juvenile northern pike.

low zooplankton abundance, correlates to a high mortality rate. The graphs were shaped in such a fashion since fish are less capable of modifying their diets at the larval life stage. Therefore, a shortage of zooplankton at the larval lifestage would correlate to a more severe impact on the larval mortality rate, than a shortage of prey may have on the mortality rate of older fish. As previously discussed, no information on zooplankton abundance has been collected from the Limestone reservoir, and thus, it was assumed that the relative abundance of zooplankton has not changed since impoundment. Therefore, this relationship is a constant mortality rate throughout the simulation. These relationships were built into the model framework users to experiment with the sensitivity of the model to changes in these relationships and for future application of the model to other reservoirs.

The third, fourth and fifth phases of the northern pike life-cycle are the juvenile, one to two year olds, and two to four year olds, respectively. The factors which affect these life phases are age dependant predation (cannibalism) by older northern pike, and an age dependant mortality rate. The predation estimates are based on the literature, and the mortality rates are dependant upon the abundance of the preferred food item utilized at that particular life stage. The abundance of northern pike in a reservoir may have a large impact for the entire fish community. As the top predator in the aquatic environment, variations in northern pike year class strength translates to community-wide effects, since northern pike predation rates influence the abundance of their own and other fish species (Frost 1954). Lawler (1965) found that the size of the food items selected by northern pike depended upon the size of the pike. Because the model does not account for growth, the predation rates used are age dependant. The predation estimates consider that older

age classes of northern pike predate upon younger age groups of their own and other species. The predation estimates for other species in the model are included in the discussions of the respective species. It has been shown that northern pike diet can vary greatly from season to season (Diana 1979, Chapman et al. 1988). However, the model did not consider the effect of changing the predation rates throughout the year. Each predation rate is dependant upon the availability of prey.

In general, juvenile northern pike have been found to feed predominantly on invertebrates (Hunt and Carbine 1951, Frost 1954), while larger pike have been found to be strongly piscivorous (Frost 1954, Seaburg and Moyle 1964, Lawler 1965, Wolfert and Miller 1978, Diana 1979, Bregazzi and Kennedy 1980). Laboratory studies have shown that pike prefer soft-rayed fishes over spiny rayed fishes (Beyerle and Williams 1968). Northern pike have been found to be capable of modifying their feeding habits/strategies in response to environmental changes (Svirskaya and Ivanova 1990, Sammons et al. 1994). However, few studies have documented northern pike diet selection over an entire year, or have been conducted on an annual basis in natural lakes or reservoirs. In addition, few studies have provided quantitative estimates for northern pike food selection on a monthly or annual basis. Many studies have documented the importance of prey items in the diets of northern pike, and ranked the prey species in order of occurrence in the diet. Diana (1979) found that in Lac Ste. Anne, Alberta, yellow perch were the most common food item, followed by spottail shiners, burbot, white sucker, lake whitefish, and walleye, respectively. In a study on Lake Windermere, Frost (1954) found that perch, followed by white sucker, spottail shiner, stickleback, pike, burbot, whitefish, tullibee, and walleye comprised pike diet in that order of decreasing importance. Lawler

(1965) found a similar order of importance of prey items in Heming Lake, Manitoba where trout perch, yellow perch, sticklebacks, spottail shiners, were the main contributors to the pike diet, while northern pike, burbot, coregonid fish, walleye and darters were found in decreasing order of importance and contributed almost negligible amounts..

Perch were found to be the predominant prey in pike diets included in studies conducted by Frost (1954), Seaburg and Moyle (1964), and Lawler (1965). Application of this model to another system, or further building on the framework of this model may require the addition of perch, if perch are present in large numbers in the system being modeled. Perch are not believed to be present in large numbers in the Limestone reservoir, and thus were precluded from model development.

In Split Lake, Manitoba, (upstream of the Limestone reservoir on the Nelson River) dietary analysis from studies conducted in 1997 and 1998 indicated that rainbow smelt and yellow perch were the most frequently preyed upon fish species, but lake whitefish, lake cisco, trout-perch, northern pike, burbot, white sucker, walleye, lake chub, darters and spottail shiner were also consumed (Lawrence et al. 1999). In the Limestone reservoir in 1999, Bretecher and MacDonell (2000) found that northern pike diet consisted of 70% rainbow smelt, and smaller proportions of lake cisco, lake whitefish, burbot, white sucker, perch, walleye and sculpin. Longnose sucker were absent from the diet (Bretecher and MacDonell 2000), however, longnose sucker at sizes suitable for consumption may not have been present in the reservoir at high numbers.

While the composition of pike diets has been analyzed by numerous authors, only Frost (1954) and Lawler (1965) have produced quantitative estimates on food items consumed by northern pike, therefore, the quantitative estimates provided by Frost (1954)

and Lawler (1965) were used for preliminary model estimates. The predation rates were age dependant, however, in general, the rates were highest for longnose sucker, followed by northern pike, lake whitefish, and walleye. This was done in order to be consistent with the relative importance of dietary items found in the studies described above.

Frost (1954) suggested that cannibalism plays only a small part in the feeding of the pike, and shows some tendency to occur more in the smaller than the large individuals. He found that pike were found in northern pike stomachs at a 1.4% frequency. Lawler (1965) found that the number of pike cannibalized increases with the size of the pike. Therefore, the rate of cannibalism used in the model framework increased with age of the northern pike. The model used a maximum cannibalism rate of 0.12 juvenile pike per month (based on estimates included in Lawler 1965). This relationship (and the other predator-prey relationships used in this model), assumed that the rate is dependant upon the prey density. Holling (1959) attributes the form of the graph in Figure 30 to the existence of predator handling time. Holling (1959) argues that as prey densities increase, handling requires an increasing proportion of the predators time. Thus, at high prey densities, the predation rate attains a maximum level and decreases with a decrease in prey abundance (Figure 30). The cannibalism rate used for the one to two year old and two to four year old age classes of northern pike were estimated by Lawler (1965) to be 0.19 and 0.15 individuals per pike per month. Similar to the cannibalism rate for juvenile northern pike shown in Figure 30, these cannibalism relationships also follow the Holling (1959) predator-prey response, and used these estimates as the maximum rate.

The other factor included in the model framework that influenced the juvenile, one to two year old and two to four year old northern pike life stages was a mortality rate. This

mortality rate included all mortality with the exception of cannibalism. The mortality rate was related to the relative abundance of the preferred food item utilized at that particular life stage. The relationship assumes that the mortality rate increased with a decrease in the relative abundance of the preferred food item utilized at that lifestage. Figure 31 shows the mortality rates for juveniles and one year to two year olds (the relationship is the same for one to two year olds and two to four year olds). The relationships used were shaped more steeply for juveniles than the mortality curves for one and two year olds and two and four year olds. This was because fish are thought to be less plastic in their diet at younger life-stages and more vulnerable to reduced abundances of their preferred food item. As fish age, it is thought that they can more readily switch to alternative prey. These curves were estimated and manipulated with model testing.

The spawning population of northern pike was comprised of the sixth and seventh life-cycle phases, northern pike age 4 to 9 and northern pike age 9 to 14, respectively. Pike generally reach sexual maturity between the ages of 4 and 5, although a wide range of ages from 2 to 5 have been reported (Scott and Crossman 1973, Machniak 1975a, Inskip 1982). Baker (1990) and Bretecher and MacDonell (2000) found that most northern pike captured in the Limestone reservoir were sexually mature by the age of five. The model assumes that northern pike spawn each year once they have reached age five.

The only factor which influences the six and seventh phases of the northern pike lifecycle is the annual mortality rate. The adult northern pike annual mortality rate in the Long Spruce reservoir was estimated by Baker et al. (1990) to be 0.28 per year in 1989.

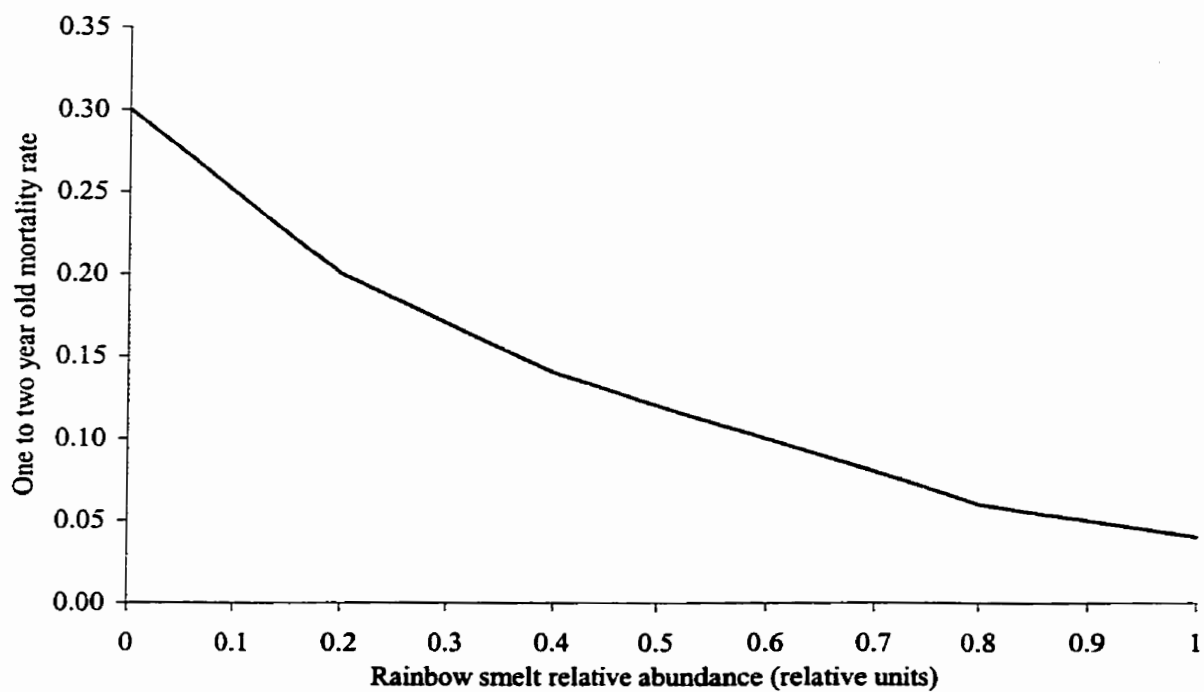
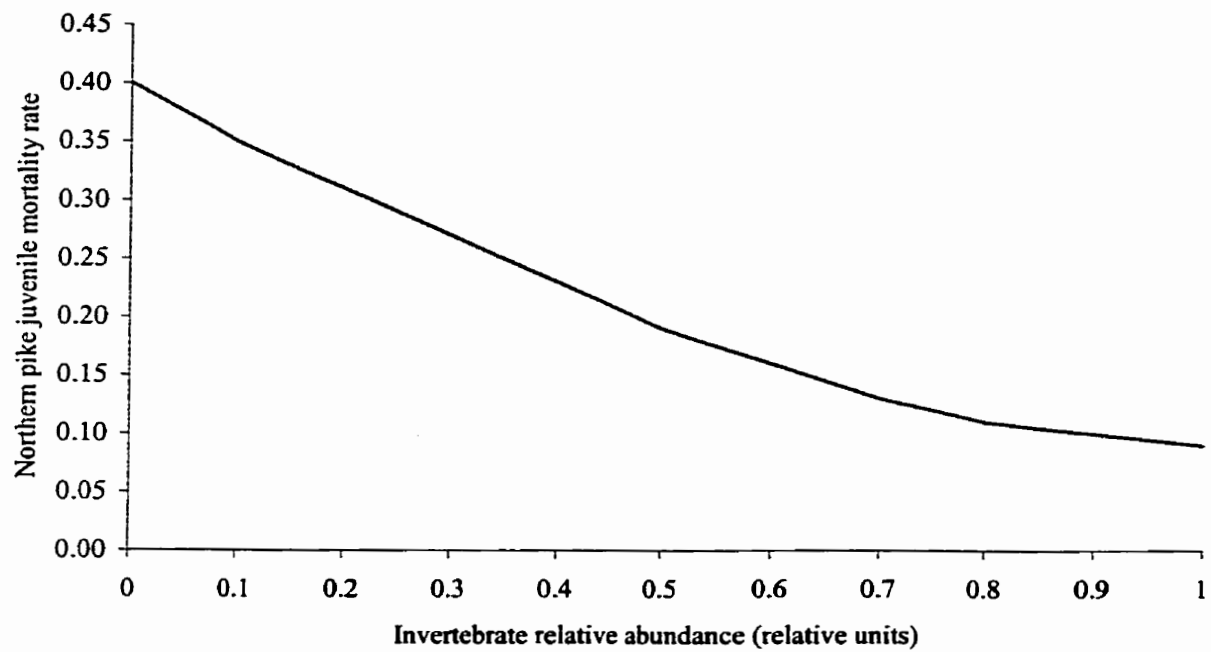


Figure 31. Relationships for northern pike juvenile and one to two year old mortality rates.

This value was used for model development (Figure 32). Diana (1983) found a similar northern pike adult mortality rate on Murray Lake, Michigan. The annual mortality rate was related to the relative abundance of smelt, the preferred food item of northern pike in the Limestone reservoir. Smelt were found by Bretecher and MacDonell (2000) to comprise 70% of the stomach contents from the Limestone reservoir. The relationship assumes that the mortality rate decreases slightly with an increase in the relative abundance of smelt (Figure 32). The rationale behind this relationship is discussed in section 3.6 (growth).

Longnose sucker

The structure of the longnose sucker sector of the model is shown below (Figure 33).

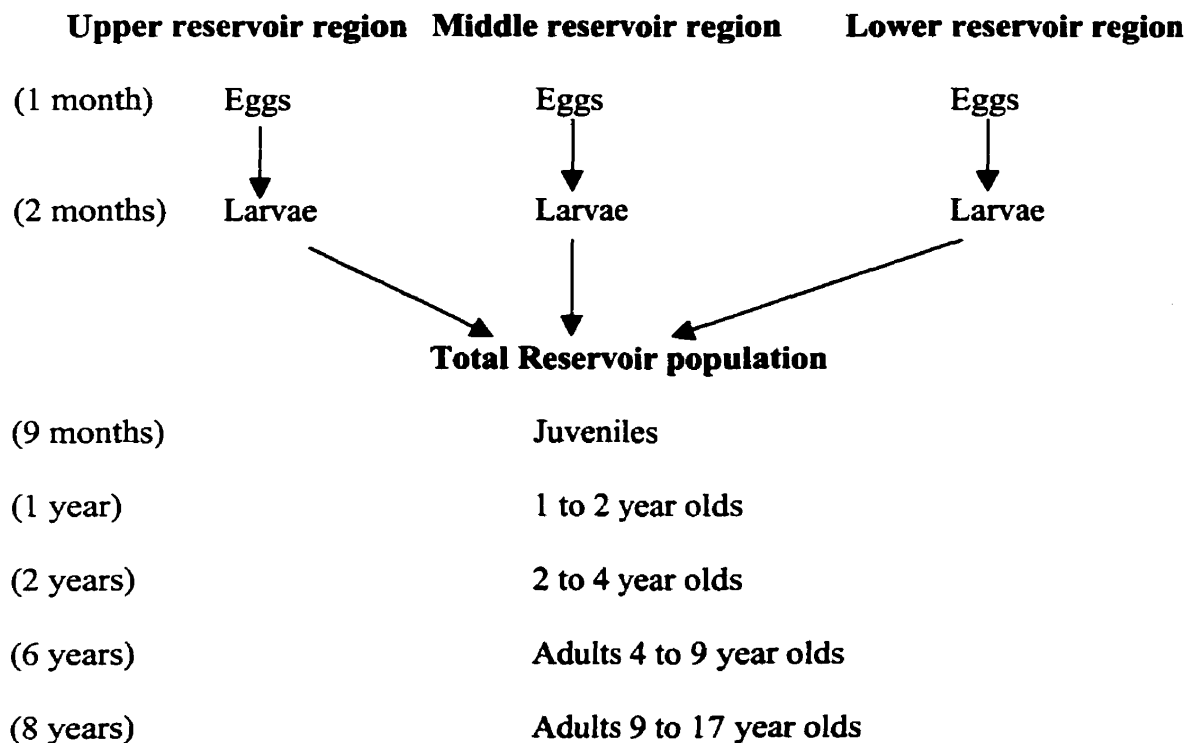


Figure 33. The structure of the longnose sucker sector of the **FISH** model.

Chapter 2 discussed the trend that has been observed in longnose sucker populations following river impoundment in northern Canada. The trend was described as a decline

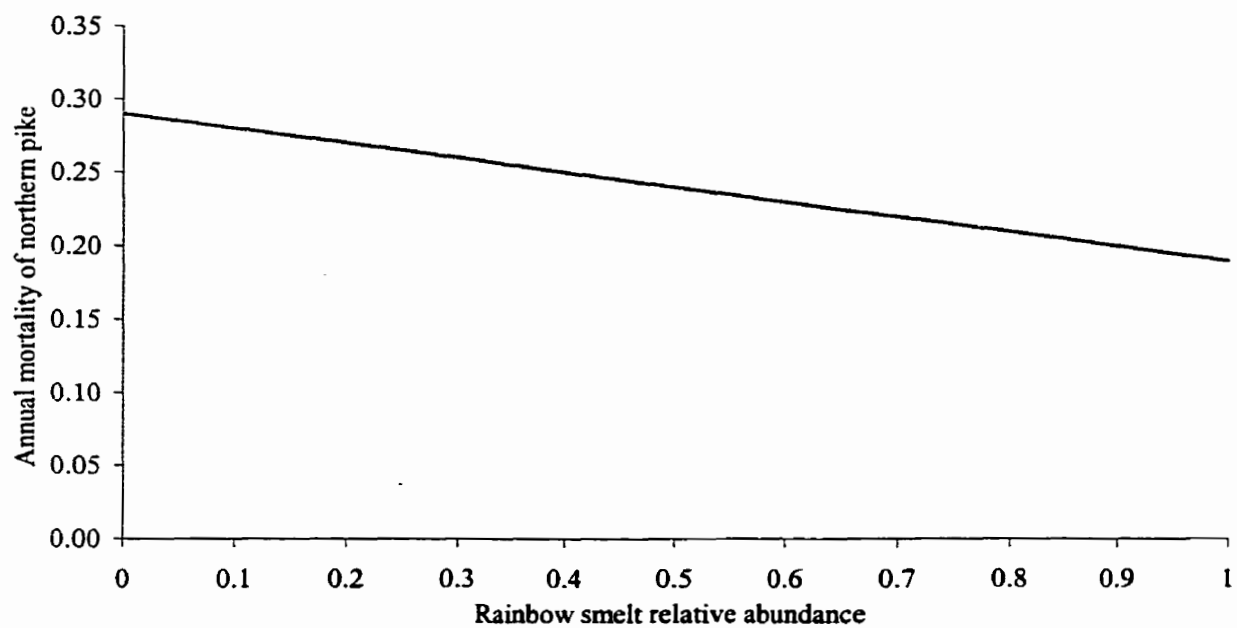


Figure 32. Relationship between northern pike annual mortality rate and the relative abundance of rainbow smelt.

in longnose sucker abundance which has been attributed to a decrease in recruitment (Deslandes et al. 1994, Bretecher and MacDonell 2000). In comparison to northern pike, relatively little literature concerning factors influencing longnose sucker populations in reservoir environments is relatively small. However, the inclusion of the longnose sucker in the model framework was deemed necessary because it has been the most abundant fish species captured in fisheries surveys of the Limestone reservoir since 1989.

The longnose sucker is the most widespread sucker in northern Canada and is found in large numbers in most cold waters (McPhail and Lindsey 1970, Scott and Crossman 1973). Longnose sucker generally spawn during spring, depending upon water temperature. Water temperatures suitable for spawning usually occur in May in the Limestone reservoir, and therefore, the model assumed that longnose sucker spawn in the fifth month of each year. In order to describe the number of eggs laid collectively by the longnose sucker population, the model used three user supplied coefficients that are assumed to remain constant throughout the 25 year simulation period. First, the model assumed that half of the longnose sucker population is female. Second, the number of eggs deposited by each female was approximated at 17,000 for longnose sucker aged 4 to 9 and 30,000 for longnose sucker aged 9 to 17. These estimates were included in Scott and Crossman (1973) who found that female longnose sucker lay an average of 17,000 to 60,000 eggs. Third, approximately 60% of longnose sucker eggs were considered fertile (Edwards 1983).

The longnose sucker is known to spawn in shallow areas of lakes and reservoirs, in waters 6 to 11 inches deep (Scott and Crossman 1973, Edwards 1983). Because longnose sucker spawn in such shallow water, their eggs may be extremely vulnerable to

fluctuating water levels (Ryan 1980, Edwards 1983). Ryan (1980) found that water level fluctuations of three metres resulted in 100% longnose sucker egg mortality. With the exception of Ryan (1980), no studies were found that correlated the magnitude of water level fluctuations to the survival of longnose sucker eggs. Edwards (1983) developed a habitat suitability index that assumed that increased water level fluctuations positively correlated to longnose sucker egg mortality. The relationship used in the model is shown in Figure 34, and was based upon the habitat suitability index developed by Edwards (1983).

In addition to the potential effects of fluctuating water levels on longnose sucker eggs, fluctuating water levels may also impact the mortality of longnose sucker larvae. After hatching, longnose sucker larvae undergo a period of inactivity. It is during this period that the larvae may be susceptible to water level fluctuations (Edwards 1983). Ryan (1980) found that reservoir drawdowns in June and July (before larvae move to deeper water) may influence larval mortality. The relationship used in the model is shown in Figure 35. Similar to the relationship in Figure 34, it was based upon the habitat suitability index developed by Edwards (1983). The relationship assumed that an increase in water level fluctuations positively correlated with longnose sucker larval mortality.

Food availability has been found to be a major factor affecting larval survival (May 1974). After hatching, longnose sucker larvae have been found to feed on zooplankton (Crawford 1923, Rawson and Elsey 1948, Scott and Crossman 1973). The model used a relationship that assumed a correlation between the mortality rate of longnose sucker and

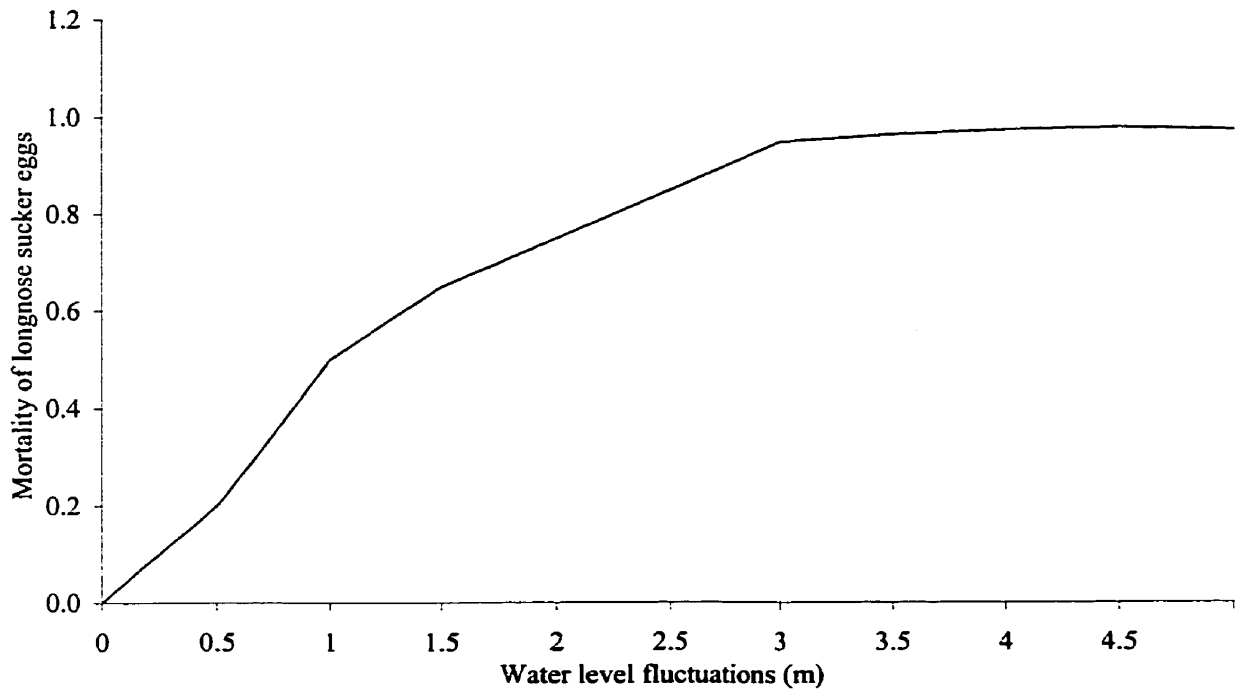


Figure 34. Relationship between longnose sucker egg mortality and water level fluctuations.

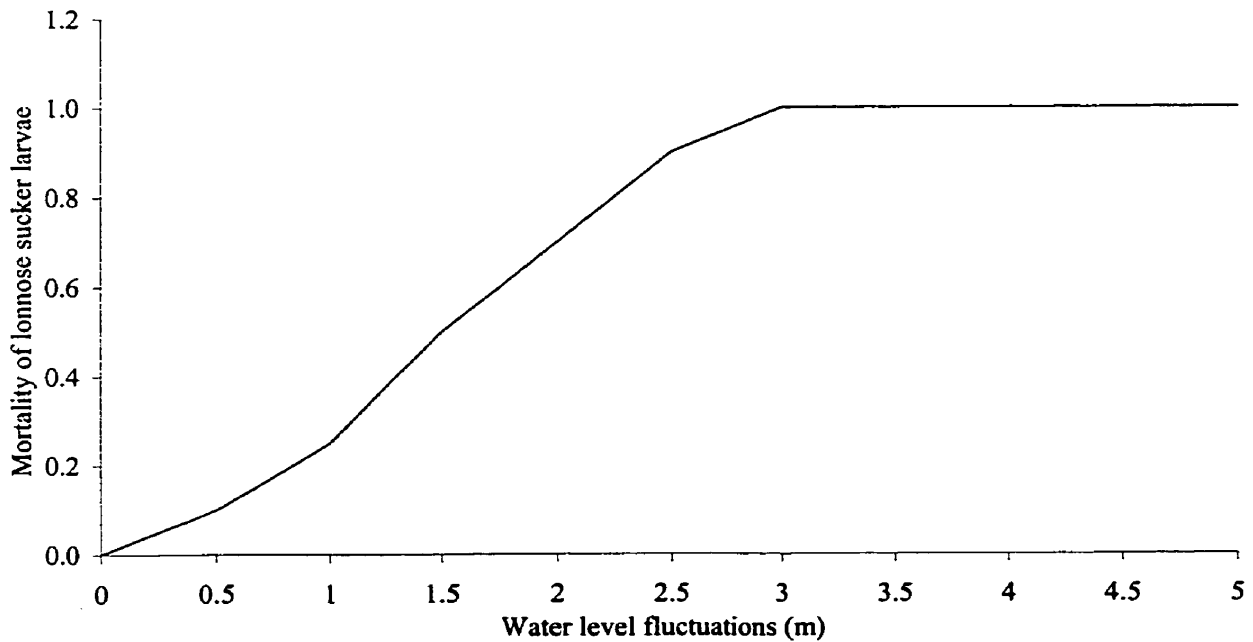


Figure 35. Relationship between longnose sucker larval mortality and water level fluctuations.

the relative abundance of zooplankton. The relationship is similar to the one used in the development of the northern pike sector of this model, and is shown in Figure 36.

Similar to the northern pike sector of the model, the third, fourth and fifth phases of the longnose sucker lifecycle (i.e., juvenile, one to two year old and two to four year old) were affected by two factors, a predation rate, and a mortality rate (which does not include predation).

Two of the species included in the model are thought to predate upon longnose sucker (i.e., northern pike and walleye). The hypothesis that the rise in northern pike populations following impoundment may increase the predation rate on longnose sucker and contribute to the decreasing trend observed in longnose sucker populations following impoundment is plausible. Cook and Bergesen (1988) mention that the introduction of northern pike was effective in controlling the abundance of longnose sucker in Eleven Mile Lake reservoir in Colorado. Colby et al. (1987) report a spectacular increase in the abundance of white sucker following the reduction of northern pike populations in Hemming Lake, Manitoba, and Harriet Lake, in Minnesota.

As previously discussed, although many authors have examined northern pike diet, few authors have quantifiably estimated the number of longnose sucker found in northern pike diet. The predation rates used in the model were, in general, highest for northern pike predation on longnose sucker. Lawler (1965) estimated that one and two year old northern pike consumed an average of 0.20 white sucker juveniles per month. Since predation rates were found to vary with size of the pike (Frost 1954, Lawler 1965) 0.20 white sucker one to two year olds (two to four year old northern pike), and 0.24 white sucker two to four year olds (for adult northern pike) were the rates used in the model.

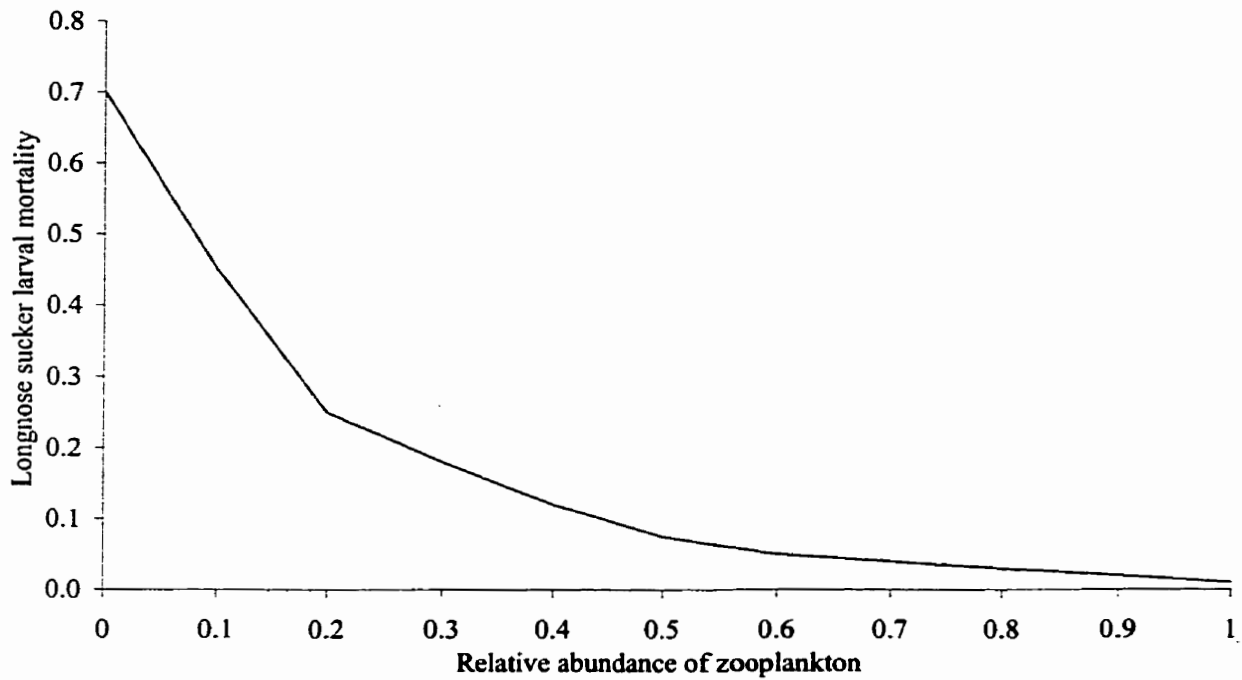


Figure 36. Relationship between longnose sucker larval mortality and the relative abundance of zooplankton.

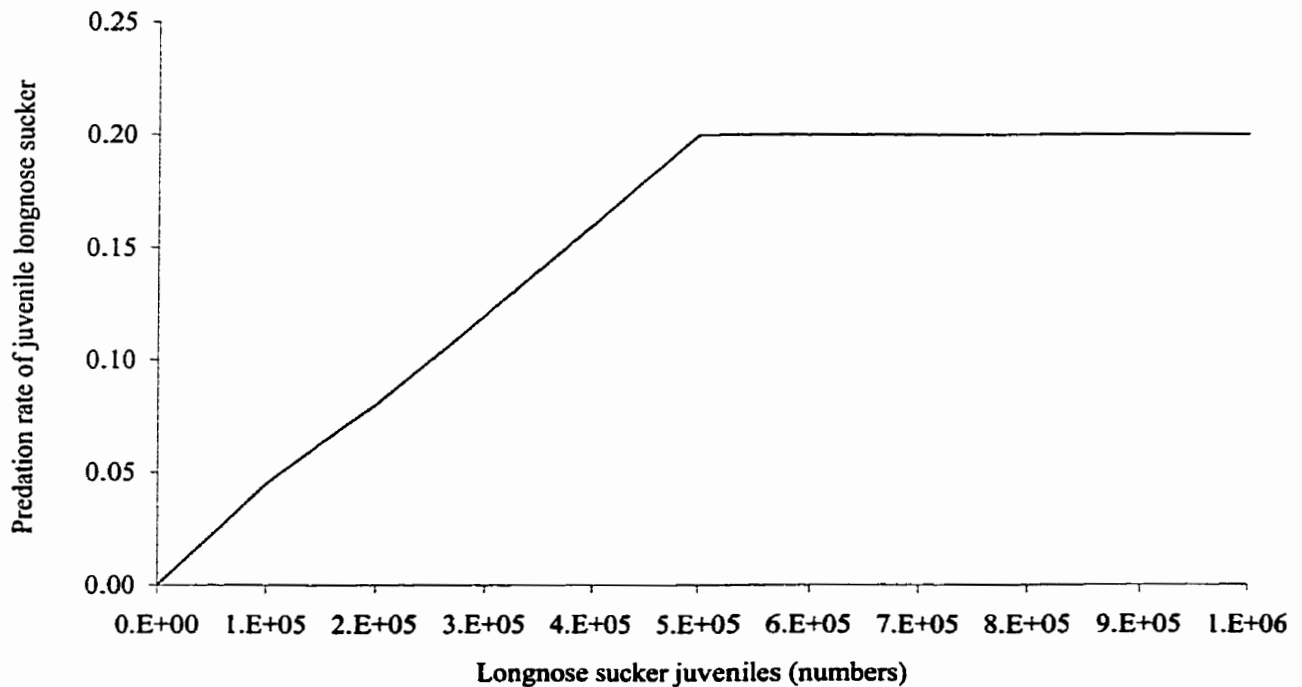


Figure 37. Relationship between the predation rate of juvenile longnose sucker and the number of juvenile longnose sucker.

The relationship provided in Figure 37 shows the juvenile predation rate. This relationship is similar to the cannibalism rate for northern pike in Figure 29, which follows the type II Holling (1959) model of predator prey interactions. The relationship, shown graphically in Figure 37, used the 0.20 average consumption rate as the maximum rate, and that this rate decreases with decreasing abundance of longnose sucker juveniles.

Additional predation on longnose sucker from walleye was included in the model framework. It is known that the diet of walleye is comprised mostly of fish. However, the rate at which they consume different fish species is difficult to estimate due to the difficulty in identifying fish to species from walleye stomachs. Due to this difficulty, a large proportion of the contents of walleye stomachs are classified as “unidentifiable fish remains”. No longnose sucker were identified from walleye stomach contents in the Limestone reservoir (Bretecher and MacDonell 2000). Although this does not mean that longnose sucker are not consumed by walleye, it does not provide the basis for an estimate. Therefore, the rate used was a conservative estimate, half the predation rates of northern pike. A further description of walleye predation is discussed in the walleye section.

Invertebrates have been found to be the preferred food item for longnose sucker (Ryan 1980, Rawson and Elsey 1948, Scott and Crossman 1973, Barton 1980 and Baker 1990). Like the mortality rate used for northern pike juveniles, one to two year olds and two to four year olds, the mortality rate used in the model was considered dependant on the relative abundance of the preferred food item at the particular life stage. The mortality rate which affects the juvenile, one to two year olds, and two to four year old life cycle phases of the longnose sucker population are similar. They assume that the

mortality rate of longnose sucker increases with a decrease in the relative abundance of invertebrates. The relationship for juveniles is shown in Figure 38.

In the northern part of its range, the longnose sucker generally mature at ages four to seven (Rawson and Elsey 1948, Brown and Graham 1953, Barton 1980). Scott and Crossman suggest that most longnose sucker mature sexually by the age of five. The model used age five since no estimates exist for the Limestone reservoir. The only factor that influenced the final two accumulations of longnose sucker was the annual mortality rate. No estimate has been provided for the longnose sucker annual mortality in studies of the Limestone or Long Spruce reservoirs. Baker et al. (1990) estimated white sucker mortality rate to be 0.37 in the Long Spruce reservoir. The model used this estimate and assumed that it was related to the availability of invertebrates, the preferred food item of longnose sucker. The relationship shown in Figure 39 assumed that an increase in invertebrate abundance would decrease the annual mortality rate of longnose sucker.

Lake whitefish

Machniak 1975(b) writes “the impacts of reservoirs on the reproductive biology of lake whitefish are at best ambiguous and purely speculative. The apparent plasticity in reproduction permits spawning in a wide variety of habitats. In theory, if a lake becomes subjected to impoundment and water level control, whitefish spawning success should decline – mainly as the result of shore erosion (siltation) and the potential exposure of spawning grounds to winter drawdown”.

The question concerning which factors may be responsible for fluctuations in lake whitefish populations in reservoir have long puzzled researchers (Christie 1963). Chapter 2 described trends that have been observed in lake whitefish populations in hydroelectric

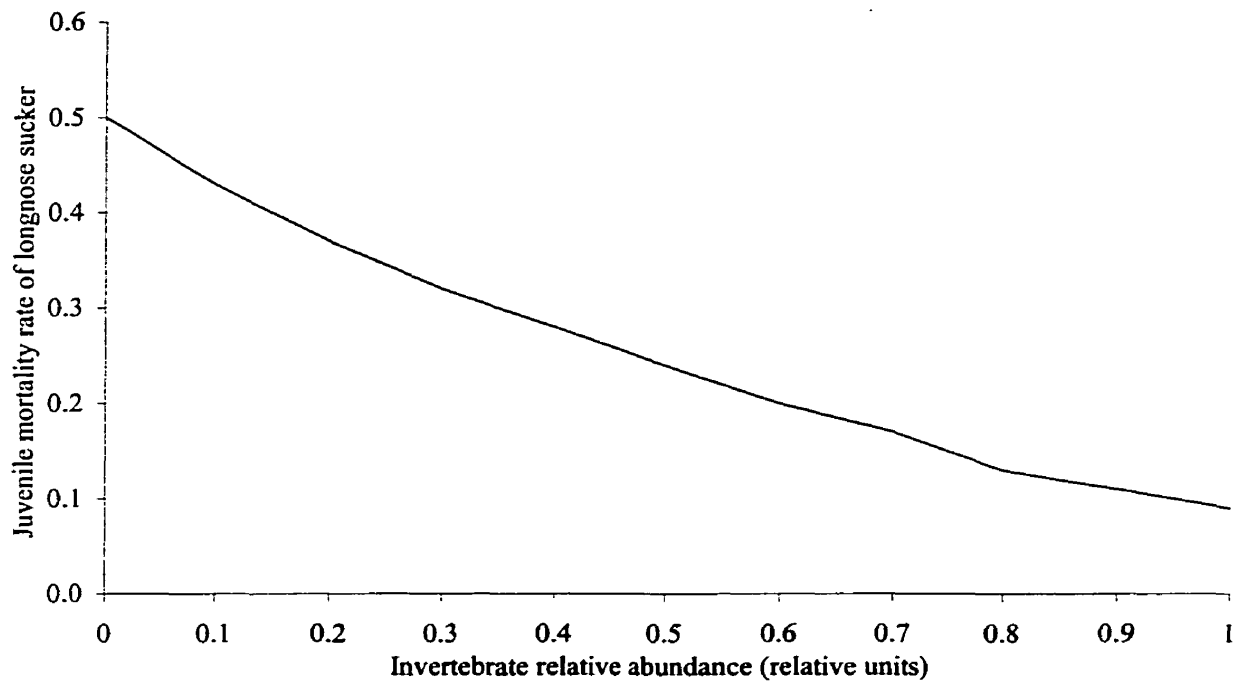


Figure 38. Relationship between longnose sucker juvenile mortality rate and the relative abundance of invertebrates.

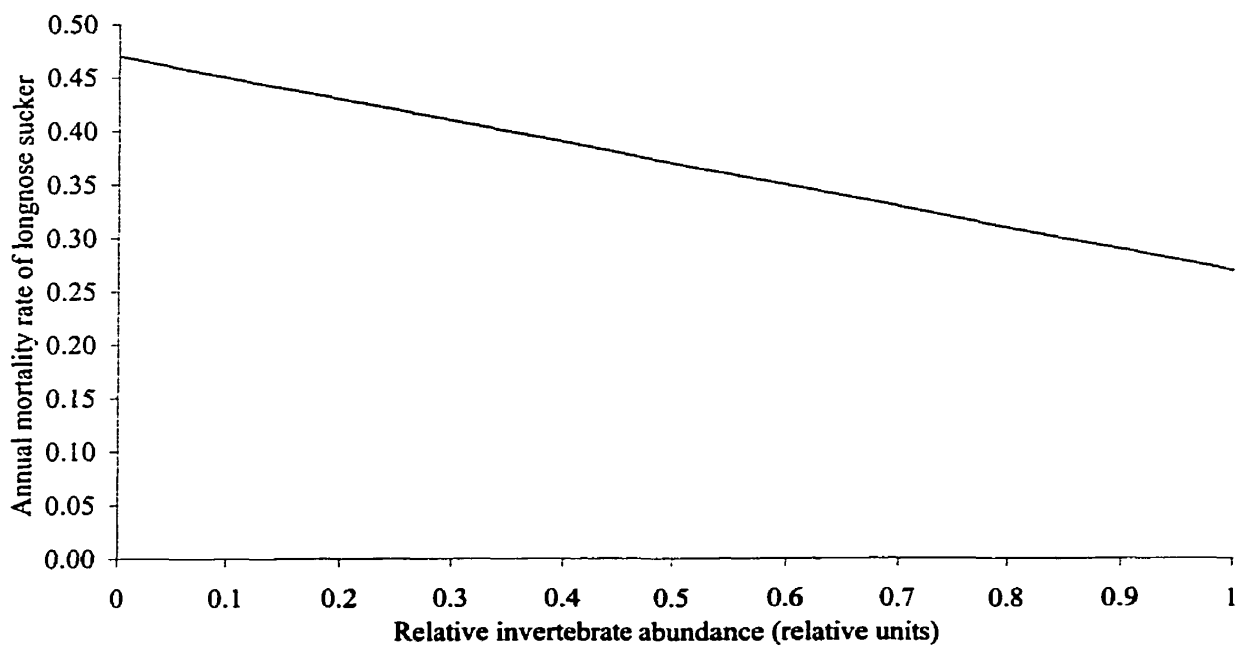


Figure 39. Relationship between the annual mortality rate of longnose sucker and the relative abundance of invertebrates.

reservoirs following river impoundment. It was discussed that the impact of reservoir development and hydro operations on lake whitefish populations may be site specific, since both increasing (Doan 1979 and Deslandes et al. 1994) and decreasing (Gaboury and Patalas 1984) trends have been noted in the literature. The fact that lake whitefish populations are potentially influenced by a large number of factors in hydroelectric reservoirs contributes to the difficulty in predicting the impact that reservoir development may have on their abundance. The structure of the lake whitefish sector of the model is shown below in Figure 40.

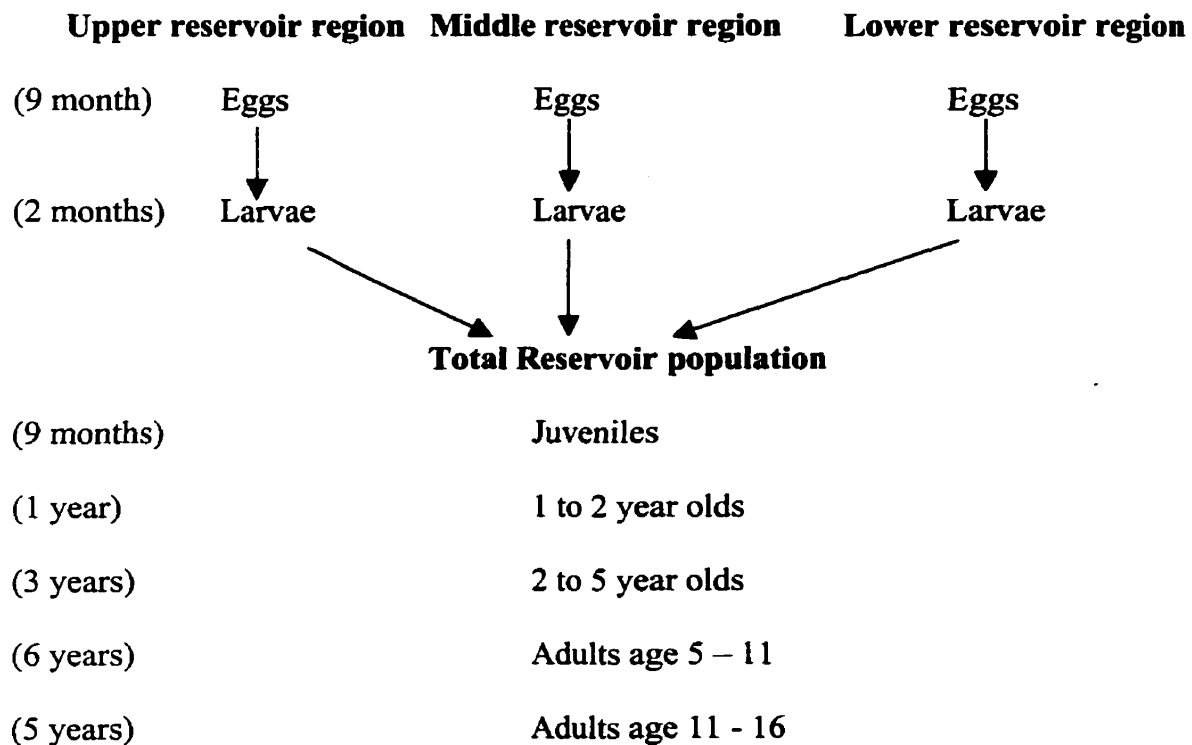


Figure 40. The structure of the lake whitefish sector of the **FISH** model.

Lake whitefish spawn during the fall, and they may select variety of suitable substrates including large rocks, gravel and sand for spawning (Scott and Crossman 1973). For model development, it was assumed that lake whitefish spawn in November (the eleventh month) and the eggs hatch in May. Like the other fish species included in

the model, a number of user supplied coefficients which were assumed to remain constant throughout the simulation, were used. First, 50% of the lake whitefish spawning population was considered to be female. Second, the model assumed a whitefish fertility factor of 0.70. Estimates from the literature concerning whitefish fertility under natural conditions are variable. Hart (1930) and Bietz (1988) estimated whitefish fertility between 0.65 and 0.75, and estimates have been reported to range between 1.0 and 0.1 (Machniak 1975b, Jensen 1981, Jensen 1985). Thirdly, it has been discussed that the number of eggs laid per female increases with size of the whitefish (Lawler 1961, Christie 1963, Jensen 1985, and others). Therefore, the number of eggs that each female lake whitefish deposited was differentiated by two adult age classes. The model used estimates of 30,000 eggs per year for lake whitefish aged 6 to 11, and 60,000 for lake whitefish aged 12 to 16. Jensen (1981), in a review of many lake whitefish populations, found a large variation in fecundity, mortality rates, age at maturity, and proportion of females among different whitefish populations. The model can test the impact of changing the above user supplied coefficients.

Gaboury and Patalas (1984), Beitz (1988) and Cohen and Radomski (1993) discuss the adverse effects of water level fluctuations on the survival of lake whitefish eggs survival in hydroelectric reservoirs. However, since lake whitefish may spawn over a considerable range of depths, (from less than 1 m to 30 m) and because they can select numerous substrate types and riverine or lake conditions for spawning, the susceptibility of an individual population to change in lake level or stream flow will depend on the specific location of the spawning grounds. The location of whitefish spawning grounds have not been identified in the Limestone reservoir, making it difficult to estimate the

proportion of eggs that may be affected by fluctuating water levels. Gaboury and Patalas (1984) found that the amount of fall to late spring water level drawdown and the year-class strengths of coregonid fish species were inversely related. They found that a marked overwinter drawdown reduced lake whitefish hatching success by dewatering spawning areas and dessicating their eggs. Cohen and Radomski (1993) correlated high water level fluctuations with reduced levels of lake whitefish commercial fish catch in Rainy Lake and Namakan Reservoir. This inverse relationship was also noted by Machniak (1975b). The relationship between water level fluctuations and lake whitefish egg mortality due to water level fluctuations is provided in Figure 41. Because lake whitefish eggs are laid during fall and have an incubation period of seven months, they may be susceptible to the settling out of sediments over their eggs (Miller 1952, Hartman 1973, Machniak 1975b). Anderson and Smith (1971) found that increased silt deposition was believed to be the cause of reduced egg survival in Coregonid species. Christie (1963) suggested turbidity and siltation as one of the important factors limiting egg survival. Fudge and Bodaly (1984) correlated the amount of sedimentation on whitefish eggs to year class strength in Southern Indian Lake, Manitoba. These authors found that a positive correlation between lake whitefish egg mortality and sediment levels. The relationship used in the model is shown graphically in Figure 42.

Low zooplankton abundance, at times critical to larval fish survival can result in heavy larval fish mortalities (Teska and Behmer 1981, Taylor and Freeberg 1984). Zooplankton availability has been found to be a critical factor influencing whitefish survival (Taylor and Freeberg 1984, Brown and Taylor 1992) since after hatching, lake whitefish larvae feed predominantly on zooplankton (Reckahn 1970, Scott and Crossman

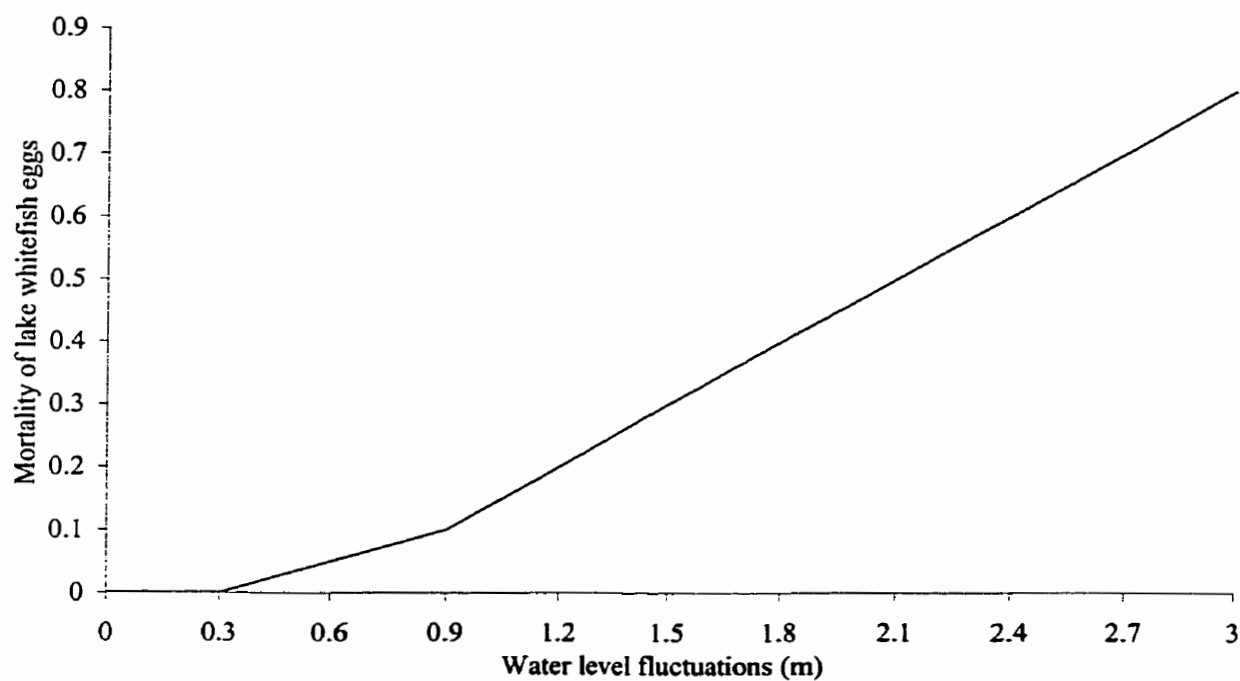


Figure 41. Relationship between the mortality of lake whitefish eggs and water level fluctuations.

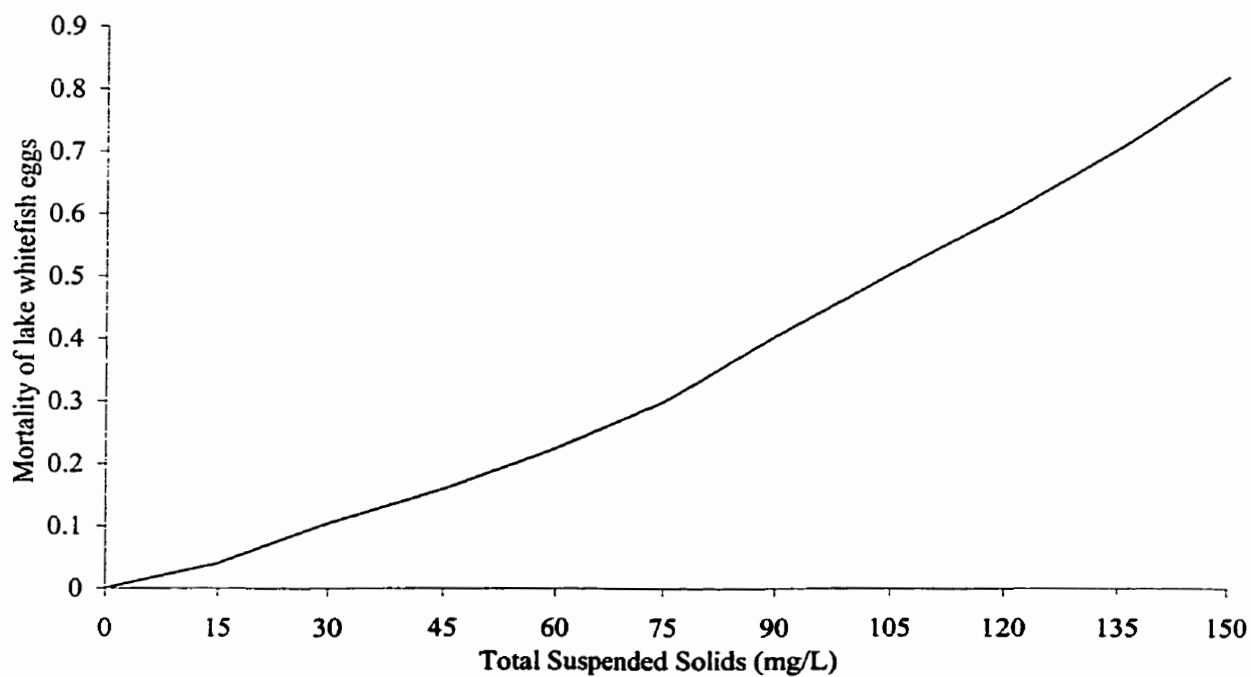


Figure 42. Relationship between the mortality rate of lake whitefish eggs and total suspended solids.

1973, Jensen 1981, Jensen 1985). Like the relationships for the other species included in the model, it was assumed that the larval mortality rate was related to the relative abundance of zooplankton. The relationship between zooplankton abundance and lake whitefish larval mortality rate is shown in Figure 43.

Smelt affect the dynamics of various fisheries by providing food for some fish species, while predating upon eggs and larvae of other fish. The colonization of smelt on a water body has been associated with lake whitefish recruitment failure (Christie 1972, 1974, Crowder 1980). Anderson and Smith (1971) found that rainbow smelt consumed up to 17% of the available lake cisco larvae in Nipigon Bay, Lake Superior. Loftus and Hulsman (1986) found that rainbow smelt consumed an average of 8.4 individual lake whitefish larvae per day in Twelve Mile Lake, Ontario in early spring. These authors reported that the combined effect of natural mortality and smelt predation may result in 100% mortality (Loftus and Hulsman 1986). The relationship between whitefish larval predation and smelt that was built in to the model assumes that smelt may consume approximately eight lake whitefish larvae per day, or 240 per month.

Like the models developed for northern pike and longnose sucker the juvenile phase, one to two year old, and two to four year old life phases of lake whitefish are affected by a predation factor and a mortality rate (which excludes predation).

The impact that impoundments have on the food resources of the lake whitefish is complicated by the lake whitefish's generalized feeding habits. Lake whitefish are known to feed upon a variety of invertebrates (McPhail and Lindsey 1970, Scott and Crossman 1973, Machniak 1975b and Baker 1990), and after impoundment, some components of invertebrate populations increase, while others decrease. Impoundment can result in a

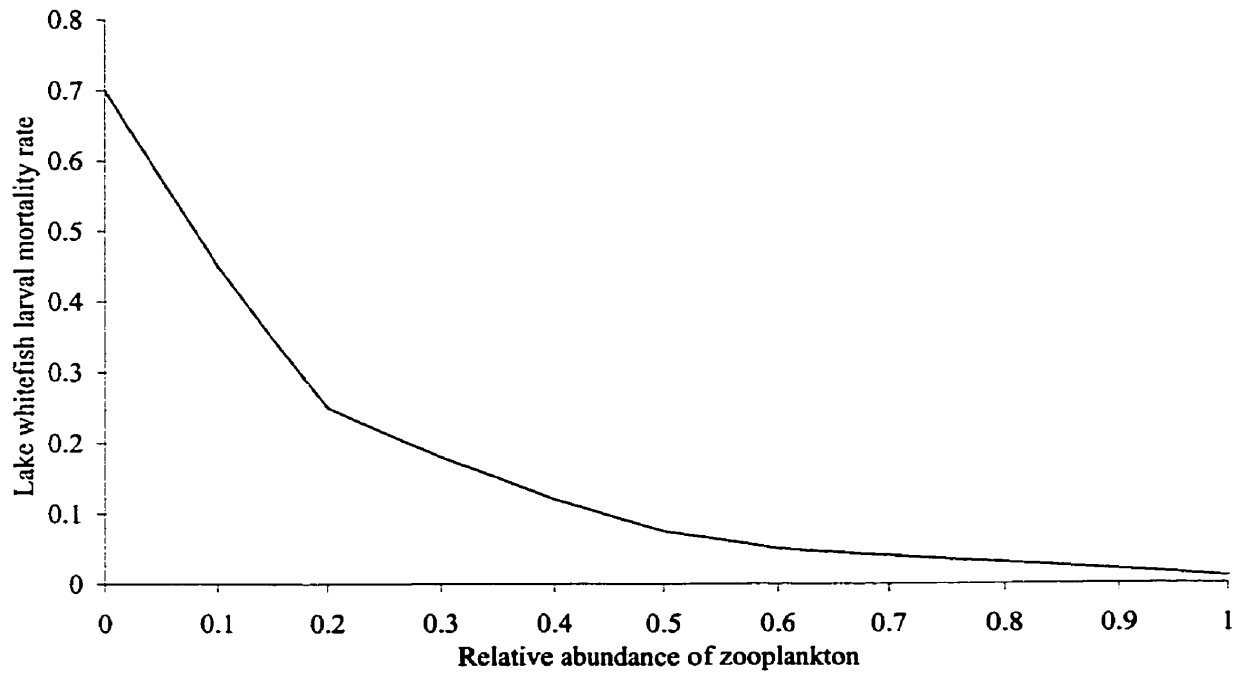


Figure 43. Relationship between lake whitefish larval mortality and the relative abundance of zooplankton.

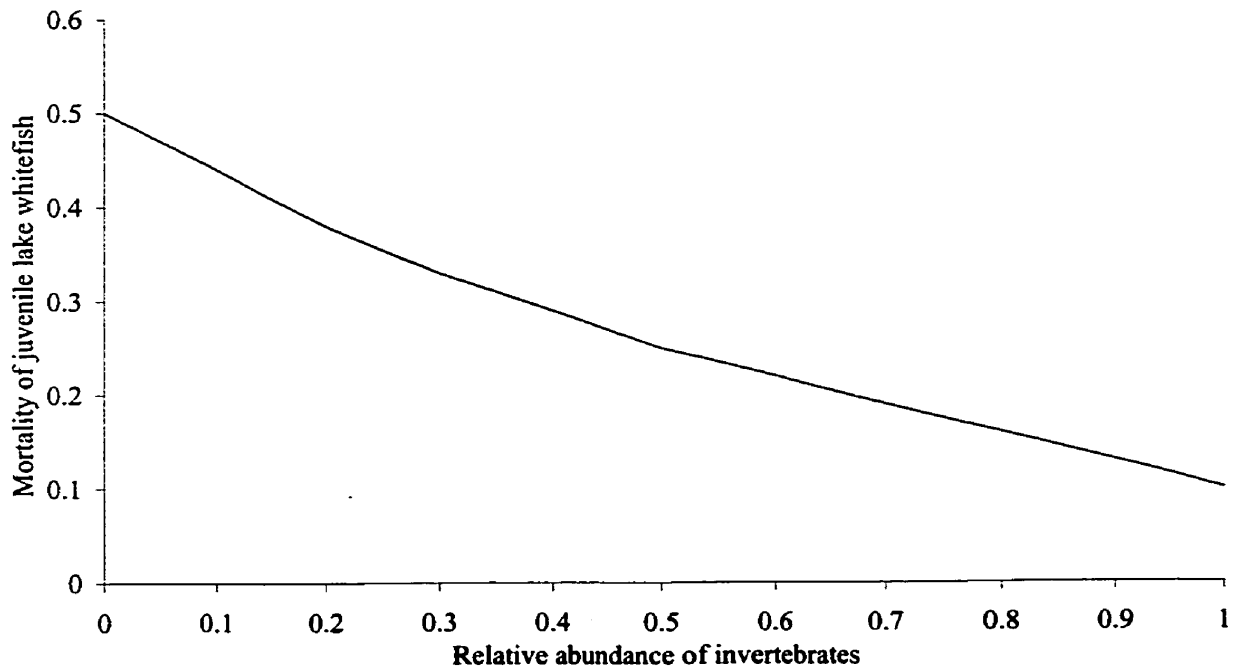


Figure 44. Relationship between the mortality of juvenile lake whitefish and the relative abundance of invertebrates.

wide variety of effects upon whitefish food supplies, the magnitude of which will depend upon the location, type of development, extent of regulation and other factors. Like the relationships used for other fish in the model, the mortality rate was based upon the relative abundance of their preferred food item (invertebrates) in the Limestone reservoir. The relationship assumed that the mortality rate for these three life cycle phases will increase with a decrease in the number of invertebrates (Figure 44). The natural mortality fraction for juveniles, one to two year olds two to five year olds is similar to the relationship shown in Figure 44.

As previously discussed, lake whitefish are thought to be predated upon by northern pike. As a result, northern pike abundance is thought to influence the overall abundance of lake whitefish in reservoirs (Machniak 1975b, Jensen 1981, Jensen 1985). Lawler (1965) found that northern pike in the size range of one year olds in this model, predated upon juvenile lake whitefish at a rate of 0.01 juveniles per pike per month. Lawler (1965) speculates that this low rate of predation may be due to the differences in habitat that the two fish species occupy. The relationship is shown in Figure 45. Lawler (1965) also estimated that northern pike predated upon lake whitefish one to two year olds (two to four year old northern pike, and lake whitefish two to five year olds (Adult northern pike) at a maximum rate of 0.008 per pike per month, and 0.008 per pike per month, respectively. The relationships are similar in shape to Figure 45.

Similar to establishing a predation rate on longnose sucker by walleye, it was difficult to estimate walleye predation rate on lake whitefish. Lake whitefish comprised a very small fraction of walleye diet from the Limestone reservoir in 1999, (Bretecher and MacDonell 2000). However, many of the walleye stomach contained unidentifiable fish

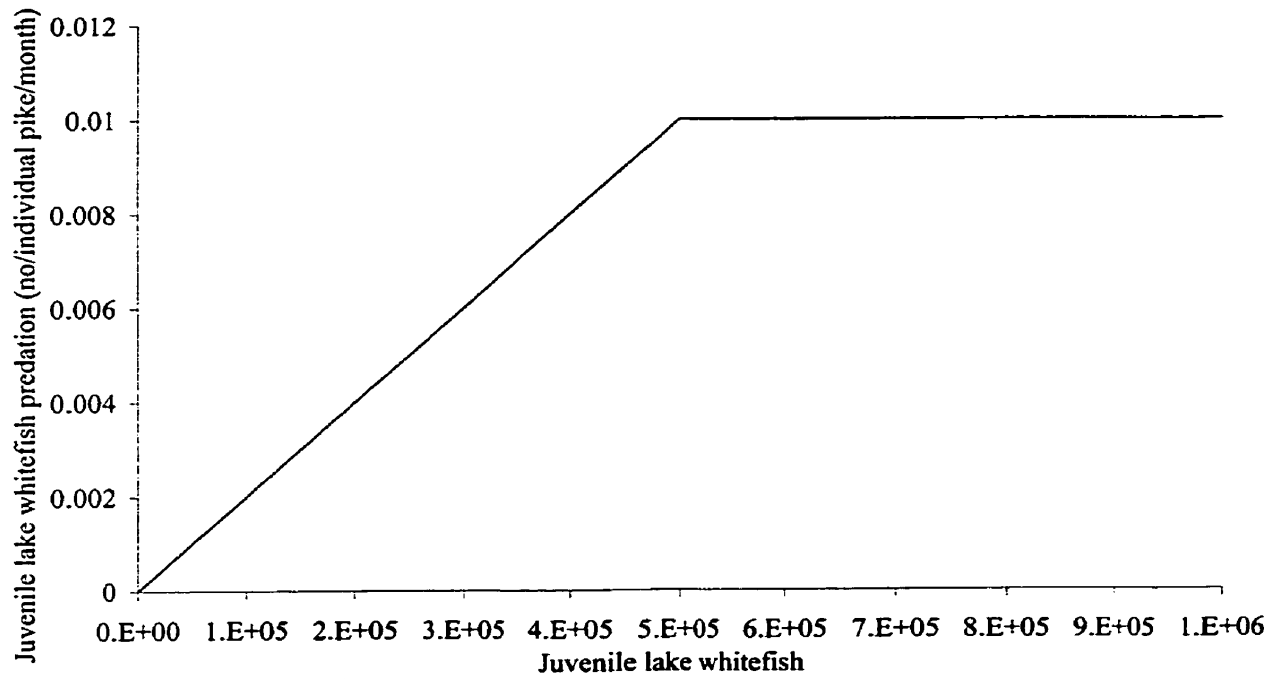


Figure 45. Relationship between the number of juvenile whitefish and the northern pike predation rate.

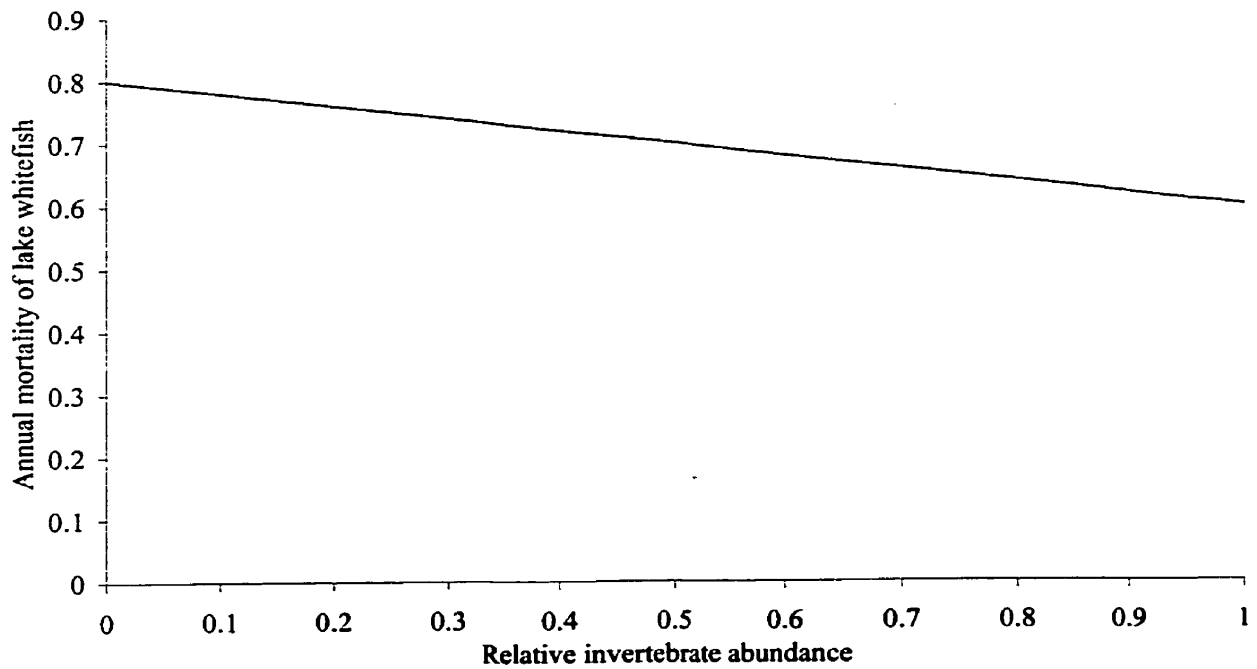


Figure 46. Relationship between the annual lake whitefish mortality rate and relative invertebrate abundance.

remains. Therefore, the rates used were conservative estimates, half the estimates used for northern pike at 0.005 lake whitefish per month. Similar to the other predation rates used in the model it followed the Holling (1959) distribution. A further description of walleye diet is discussed in the walleye section of this Chapter.

Scott and Crossman (1973) estimate that lake whitefish reach sexual maturity at 6 years of age at high latitudes (Scott and Crossman 1973). The last two stocks of lake whitefish are: lake whitefish aged 5 to 11 and lake whitefish age 11 to 16. Once lake whitefish reach six years of age, the model assumes that whitefish are sexually mature. Data from the Limestone reservoir suggests that most lake whitefish are sexually mature at age 6 (Baker 1990). It has been shown that lake whitefish vary greatly in their life history parameters (Jensen 1985). Baker et al. (1990) estimated the lake whitefish mortality rate in the Long Spruce reservoir at 0.45. This mortality rate is comparable to rates observed on Lake Michigan (Jensen 1981). The mortality rate was related to food availability in a similar manner as the mortality rates calculated for northern pike and longnose sucker. The relationship is shown in Figure 46 and assumed that the mortality rate was related to the relative abundance of invertebrates in the reservoir.

Walleye

As discussed in Chapter 2, walleye abundance in many hydroelectric reservoirs following impoundment increases over time (Jenkins 1970, Doan 1979, Bennet and MacArthur 1990, Bretecher and MacDonell 2000). The structure of the walleye model is provided in Figure 47.

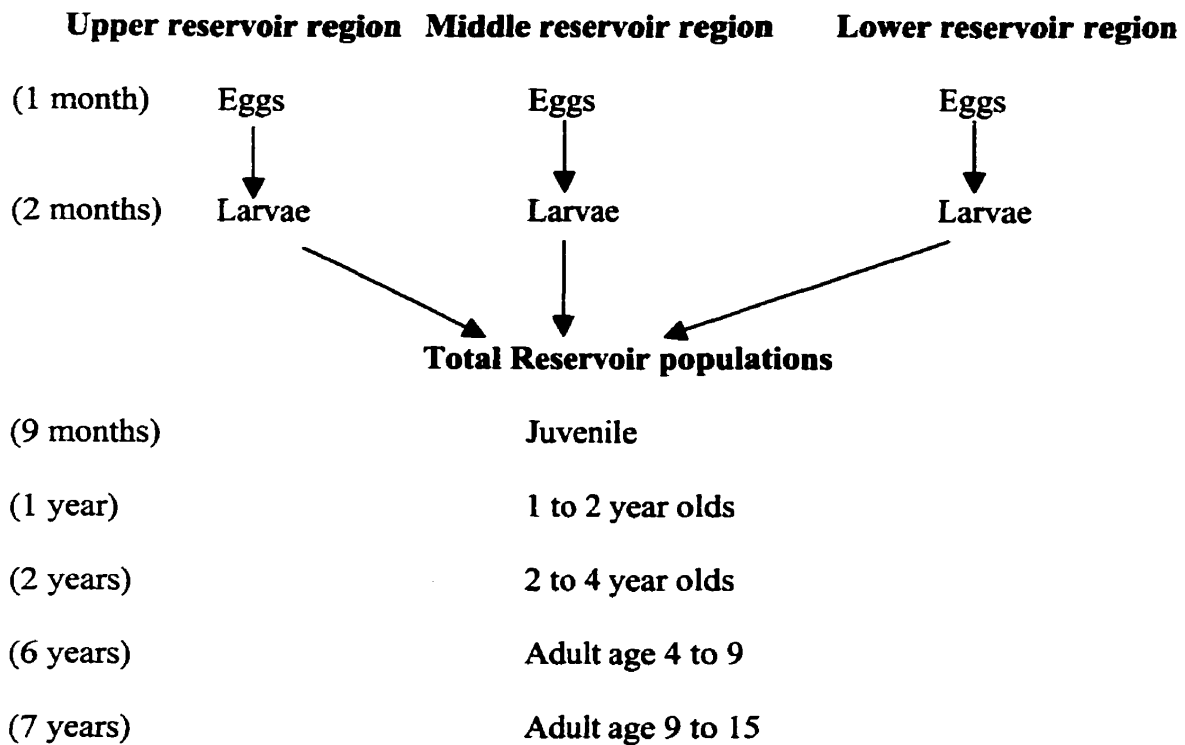


Figure 47. The structure of the walleye sector of the **FISH** model.

Like northern pike and longnose sucker, the walleye is a spring spawning fish species (Scott and Crossman 1973). To describe the number of eggs laid by walleye, three user supplied coefficients were used which remained constant for the entire simulation. First, like the northern pike, longnose sucker and lake whitefish sectors of the model, half the walleye spawning population was assumed to be female. Secondly, estimates of walleye fecundity in the scientific literature are variable. Most estimates included in Machniak (1975c) range between 30,000 and 600,000 eggs per female. Machniak (1975c) and Jensen (1989) discuss that like the other fish species included in the model, walleye fecundity is related to fish size (i.e., large fish lay more eggs than smaller fish). Therefore, 30,000 eggs were considered to be deposited by walleye age five to nine, and assuming that larger, older fish are more fecund, 50,000 eggs were used for females age nine to 15. The third density independent factor which influences the number of viable

eggs is the fertilization rate. Estimates of fertility in the natural environment range between 20.1 to 95.3 percent, with the average being 72 percent (Scott and Crossman 1973, Machniak 1975c, Jensen 1989). Seventy percent was used as the model input due to the wide ranges of values reported.

It is believed that walleye reproduction in hydroelectric reservoirs improves over time as suspended sediment in the water column decreases and coarse materials in the upper part of the reservoir become exposed (Erickson 1972). Erickson (1972) stated that the substrate in a reservoir requires five or more years of wave washing action to produce clean gravel bars, suitable for walleye reproduction. Similarly, Jenkins (1970) and Bennett and McArthur (1990) correlated reservoir age to an increase in walleye numbers and believed that the increase in walleye abundance as reservoirs age may be attributed to the improvement in the quality of spawning substrate. A walleye spawning quality factor was built into the model which assumed an increase in egg survival over time. This factor assumed that walleye spawning quality improves after 5 years, and reaches a maximum 15 years after impoundment.

The depth that walleye lay their eggs may be a critical factor influencing their success in hydroelectric reservoirs. A variety of depths have been reported in the scientific literature. For example, walleye were reported by Derksen (1967) to spawn in relatively shallow water, usually between 0.9 to 1.3 m in depth. Similarly, Niemuth et al. (1959) reported that walleye eggs are mostly deposited in water less than 0.6 m deep and no more than 1.2 m deep. If walleye were spawning in shallow water as discussed above, then it would be hypothesized that water level fluctuations may have detrimental effects on the survival of walleye eggs.

It has also been discussed that the walleye pattern of spawning appears to be adapted for a variety of habitats, and that walleye may be less specialized and less restricted in the their depth of spawning (Machniak 1975c). Priegel (1970) and Johnson (1961) discussed that water level fluctuations during the spawning period were not an important influence on walleye year-class strength. The authors write that spawning usually occurs in depths great enough that changes in water levels appear to have little impact on egg survival. Conversely, Jenkins (1970) described walleye spawning in waters less than two metres in depth, and suggested that water level fluctuations may have a negative effect on walleye spawning success. Erickson (1972) suggested that fairly stable water levels or rising water levels benefit walleye during spawning and incubation, and that slow water level fluctuations produce the best walleye year classes.

The literature regarding the impact of water level fluctuations on the spawning success of walleye indicates that the impacts may be site specific and dependant upon depth of spawning. The relationship used in the model assumed that the proportion of walleye egg mortality is positively correlated with water level fluctuations (Figure 48). However, this relationship assumed that a greater fluctuation in water level must occur to affect egg mortality, relative to other spring spawning fish included in the model (i.e., northern pike and longnose sucker).

Mion et al. (1997) found that walleye year-class strength may be largely dependant upon factors that affect the larval life stage. Walleye larvae are impacted by various factors in the reservoir including natural mortality, predation, and cannibalism. Similar to the other fish species included in this model, after hatching, larval walleye are known to feed upon zooplankton. Jonas and Wahl (1998) found that starvation can directly

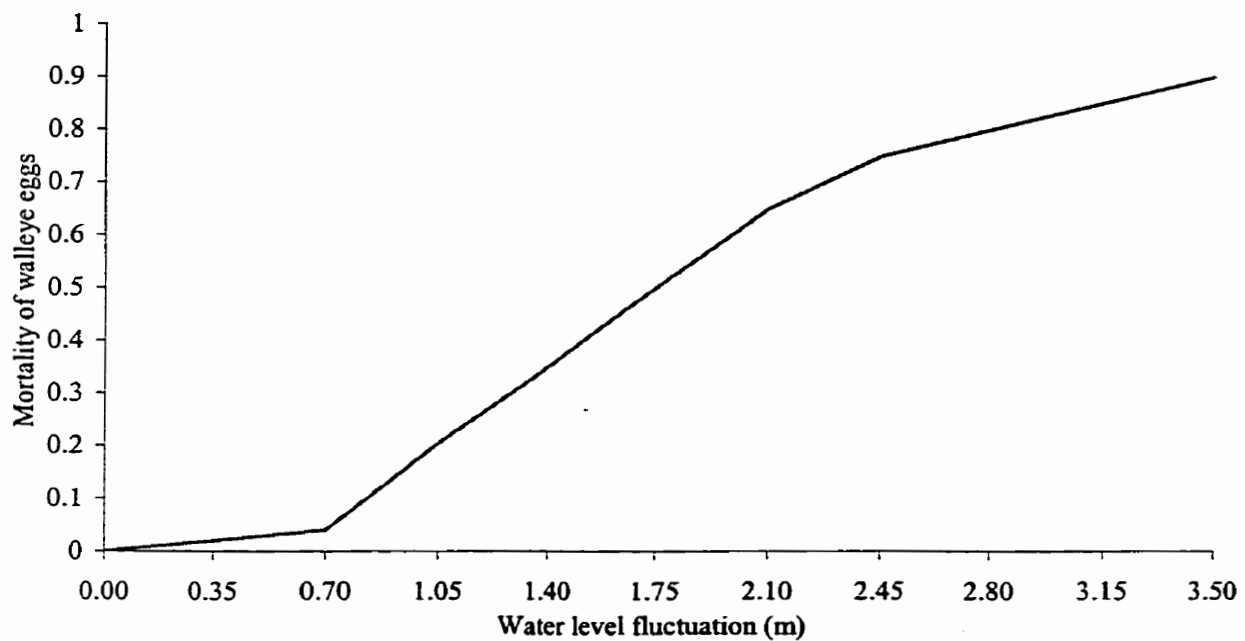


Figure 48. Relationship between the mortality of walleye eggs and water level fluctuations.

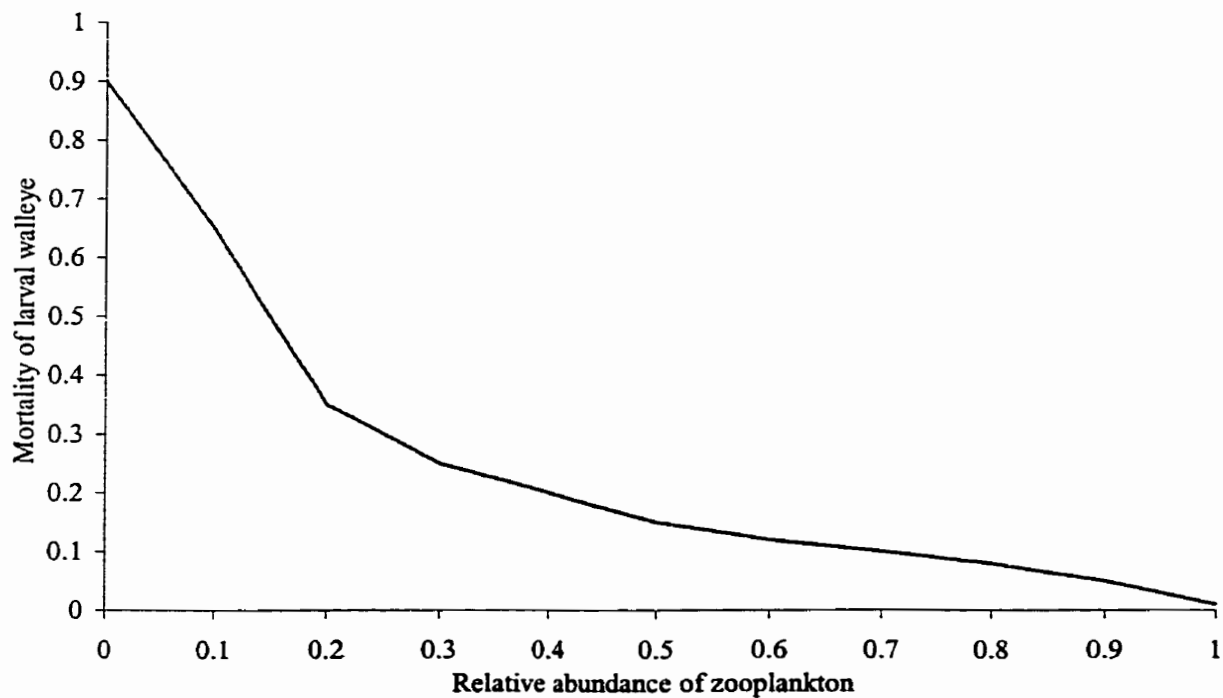


Figure 49. Relationship between larval walleye mortality and the relative abundance of zooplankton.

impact the mortality rate of larval fish. A mortality rate was based upon the abundance of zooplankton and assumed a higher mortality rate for larval walleye with a decreased abundance of zooplankton (Jensen 1989). The relationship between the abundance of zooplankton and the walleye larval mortality rate is shown in Figure 49.

The model framework considers that juvenile, one to two year old and two to four year old walleye are influenced by predation from northern pike, cannibalism and a mortality rate (independent of predation and cannibalism).

Northern pike have been found to predate upon walleye (Lawler 1965, Machniak 1975a). However, it was difficult to establish a predation rate on walleye from northern pike. As previously discussed, the predation rates used in the model for northern pike predation on walleye were the lowest when compared to the other fish species included in the model. Lawler (1965) estimated that northern pike consumed an average number of 0.0008 walleye during the years 1950-1962 over a twelve year period in Heming Lake, Manitoba. He found that walleye were rarely consumed at each size class. However, walleye were not present in high numbers in Heming Lake during this study. Bretecher and MacDonell (1999) and (2000) found that in the Limestone, Long Spruce and Kettle reservoirs that walleye contributed almost negligible amounts to northern pike diet (a further description of northern pike diet is provided in the northern pike section). The model used a low predation rate relative to the other fish species included in the model, set at 0.05 for juveniles, one to two year olds and two to four year olds. These relationships were also based on the Holling (1959) type II response of predator-prey interaction. The predation relationship for one to two year olds is provided in Figure 50.

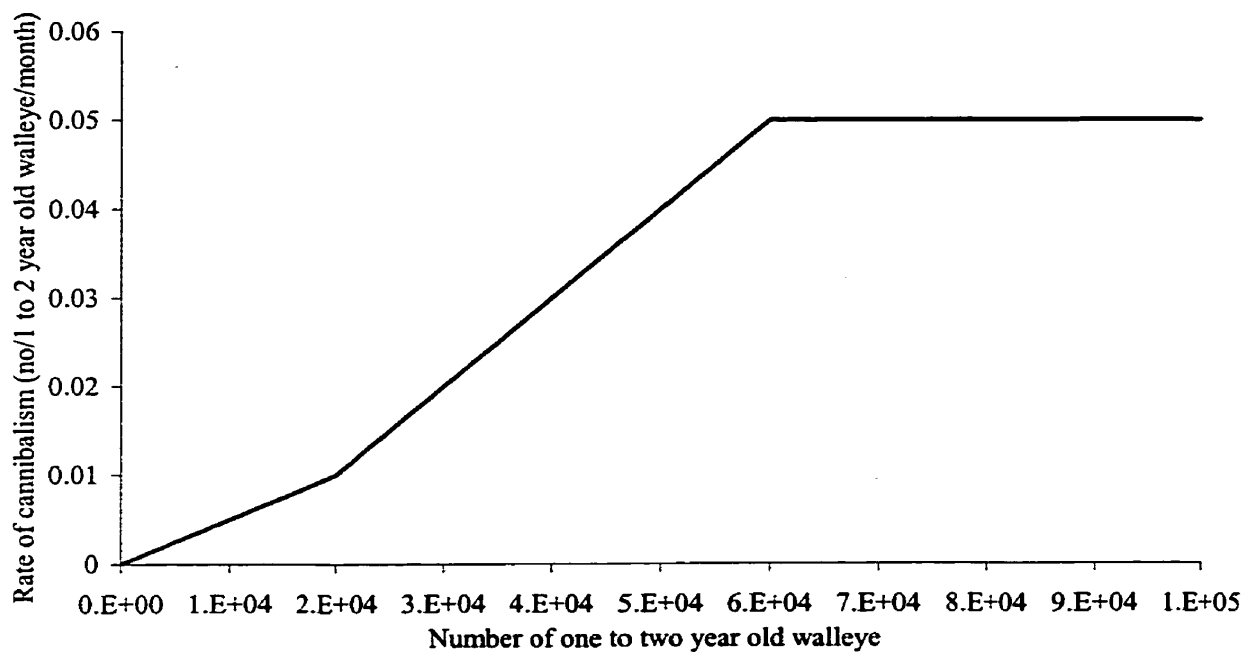


Figure 50. Relationship between northern pike predation rate per month and the number of one to two year old walleye.

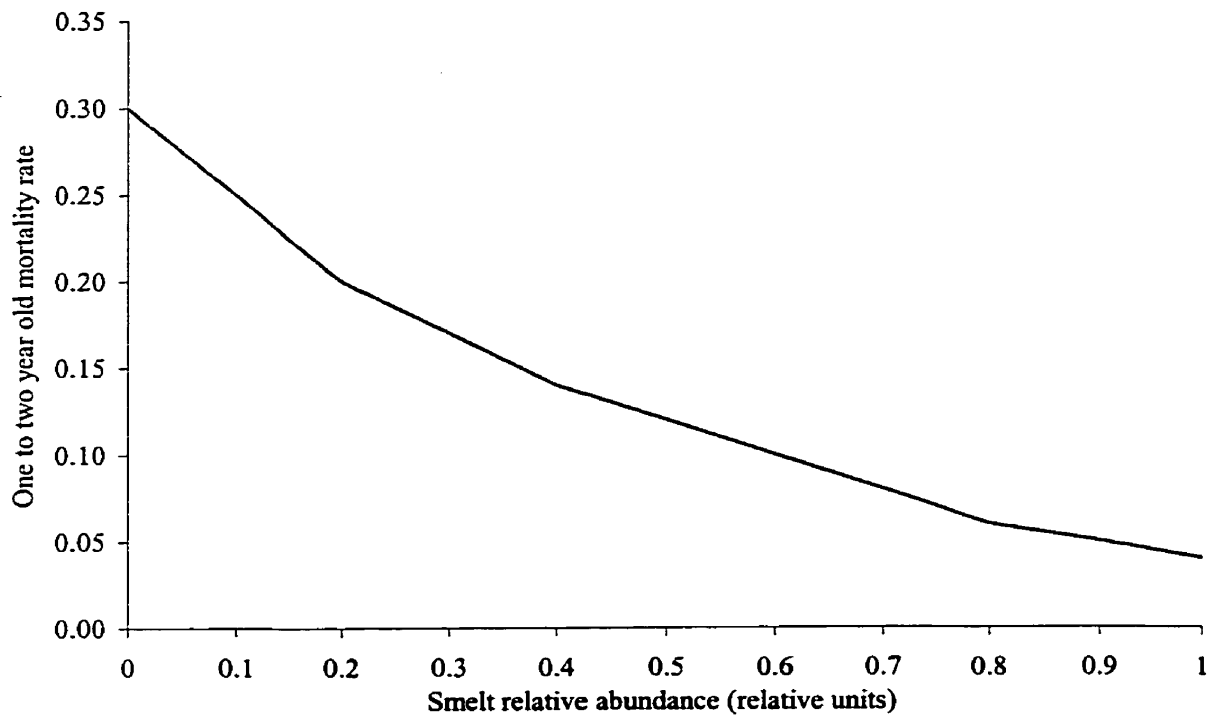


Figure 51. Relationship between walleye one to two year old mortality rate and the relative abundance of smelt.

Studies have indicated that like the northern pike, walleye are size selective predators, and thus their diet changes with age (Nielsen 1980, Knight et al. 1984, Enfalt and Wahl 1997). Before the end of their first year of life, the majority of walleye diet is thought to be comprised of invertebrates (Scott and Crossman 1973, Ritchie and Colby 1988). Therefore, the walleye juvenile mortality rate was related to the relative abundance of invertebrates in the reservoir. Once walleye have reached their first year, the walleye diet becomes comprised mostly of fish (Scott and Crossman 1973, Knight et al. 1984). Like the relationships used for other fish in the model, the mortality rate for juveniles, one to two year olds and two to four year olds are related to their preferred food item at that life-stage. The relationship included in the model assumed that the mortality rate related to invertebrates for the juvenile life-phase, and changed to the relative abundance of smelt for one to two year olds and smelt for two to four year olds. The juvenile relationship is provided in Figure 51.

Like northern pike, walleye are fish eating predators that affect their own and other fish populations in reservoir environments. Walleye are usually night feeders, strongly associating with the bottom for cover to find food (Ryder 1977). In addition, soft rayed fish species have been found to be preferred over spiny rayed fish species (Parsons 1971, Knight et al. 1984). As briefly discussed in the sections on other fish species, estimating walleye predation rates on their own and other fish species is difficult for a variety of reason. First, walleye captured during gillnet surveys often do not provide good estimates of predation rates. This is because fish may remain in the net for a period of time before being removed, and frequently walleye will expel their stomach contents while trapped. In addition, many walleye which are examined for stomach contents

contain partially digested fish, which are difficult to identify to species. Hence, the contents of walleye stomachs are frequently described as unidentified fish remains.

For the model, walleye predation rates were determined relative to northern pike predation rates, and took into consideration the order of importance that fish species included in the model have been found in dietary analyses. Bryan et al. (1995) in Lake Oahe, South Dakota found that rainbow smelt, yellow perch, and spottail shiner were the primary constituents of walleye diet. As a generalization, in water bodies where rainbow smelt or yellow perch are available, walleye appear to select these species as prey (Swenson 1977, Lyons and Magnuson 1987). Bretecher and MacDonell (2000), in a study of the Limestone, Long Spruce, and Kettle reservoirs, found that 49% of the stomachs examined contained rainbow smelt. Other species found in small percentages included lake cisco, lake chub, lake whitefish, burbot, white sucker, perch, walleye and stickleback. Bretecher and MacDonell (1999) in the Limestone forebay found that 48% of the walleye diet was rainbow smelt, and trout perch and slimy sculpin were the only other fish species identified. Due to the difficulty in finding literature from comparable environments, and since walleye appear to prey predominantly on rainbow smelt, the rates used were conservative estimates. In general, walleye predation rates were lower relative to the predation rates used for northern pike. Maximum rates of 0.05 were used for all sizes of longnose sucker lake whitefish and northern pike.

Cannibalism as a factor which regulates walleye year class strength has been well described in the literature. Chevalier (1973) and Forney (1976) found that cannibalism by adult walleyes (age five and older) on young of the year walleye was a decisive factor in the determination of walleye year class strength. Chevalier (1973) found that the loss

from cannibalism to the walleye population represented a substantial fraction of the total mortality. In addition, Chevalier (1973) found that the number of walleye cannibalized was related to the number of walleye available. Walleye recruitment on Escanaba Lake, Wisconsin, was found to be regulated by competition with, or cannibalism by walleyes, (Hansen et al. 1998). Because cannibalism can occur in the first year of life it may be significant in regulating year class size even though much higher mortality occurs at earlier stages of development. Cannibalism is most likely to affect year class size in a population where predator density is high and where there is intense competition for prey. Chevalier (1973) and Forney (1976) estimated that cannibalism may represent a significant portion of mortality for juvenile and one year old walleye. He estimated consumption of walleye 0.27 to 1.32 per adult walleye per month. These estimates would be considered high for this model. A maximum rate of 0.10 per month was used for walleye juveniles. The relationship for walleye juveniles is shown in Figure 52. This rate at high abundances was higher relative to the predation rates on other species.

In most locations in Canada, female walleye mature sexually at 4 to 5 years of age (Scott and Crossman 1973). The model used age five since most walleye in the Limestone reservoir have been found to be sexually mature by the age of five (Baker 1990). Once walleye reach five years of age the annual mortality rate is the only factor influencing their abundance. The instantaneous mortality rate for walleye in Escanaba Lake, Wisconsin was estimated at 0.61 (Chevalier 1973). A similar rate of 0.70 was calculated for walleye in Wapisi Lake, a lake in northern Manitoba. Baker et al. (1990) estimated the mortality rate of walleye in the Long Spruce reservoir at 0.65. This value, the highest value when compared to the annual mortality rate of other fish species in the

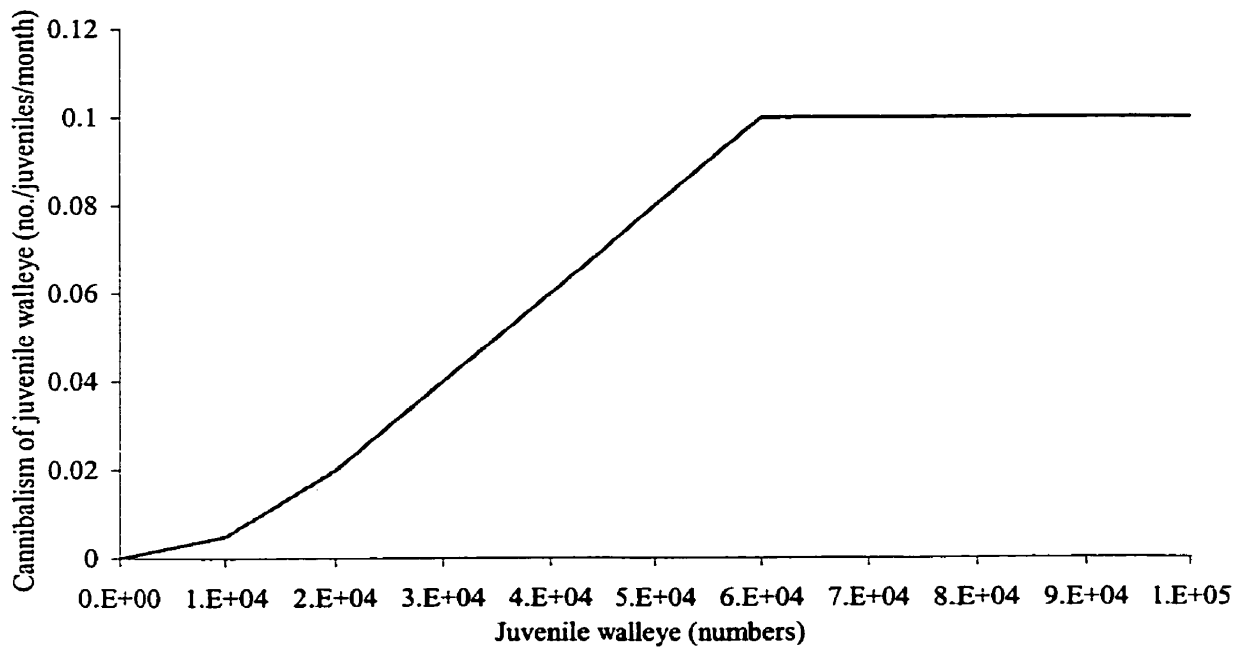


Figure 52. Relationship between walleye cannibalism and the number of juvenile walleye.

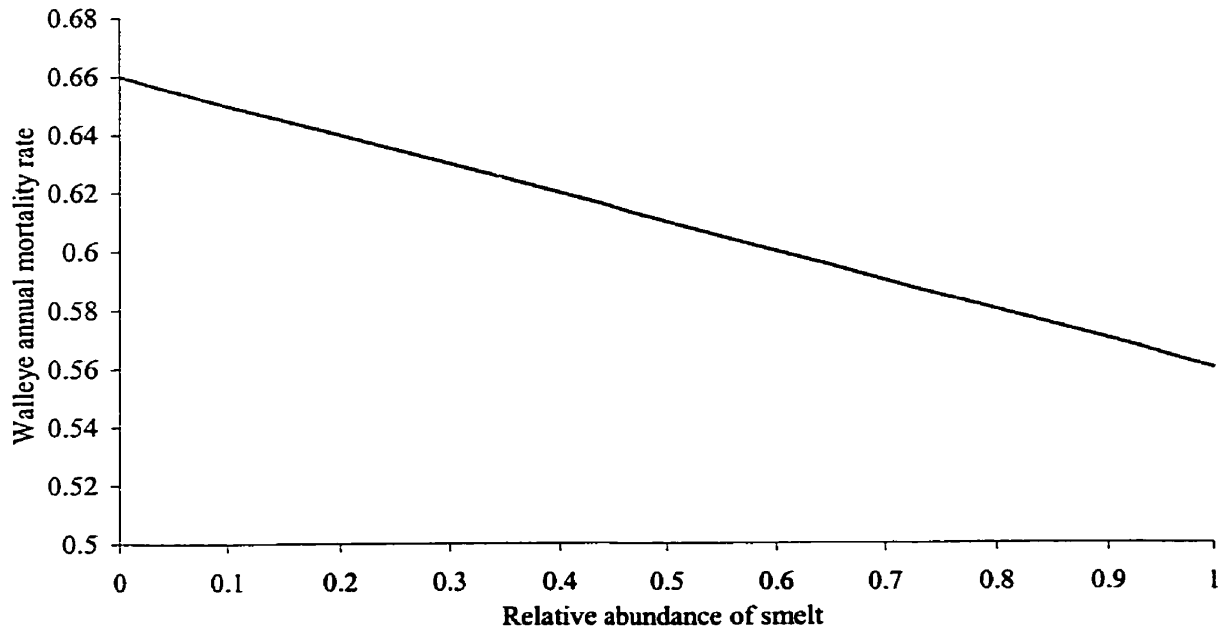


Figure 53. Relationship between annual walleye mortality rate and the relative abundance of smelt.

model, was used for the model framework. Similar to the annual mortality rates included in the model, the mortality rate was related to food availability. Adult walleye are primarily piscivorous and the abundance of forage may determine their success in impoundments (Knight and Vondracek 1993). Jones et al. (1994) found that walleye diet in Horsetooth reservoir, Colorado, changed as a result of rainbow smelt introduction. Before rainbow smelt were introduced to the reservoir, walleye fed primarily on invertebrates, salmonids and other game fishes. Once introduced, the percentage of smelt found in walleye diet increased from 19% in 1985 to 87% in 1987. This resulted in an increased growth rate of 50% in the 9 years following rainbow smelt introduction. The model used a relationship where the walleye mortality rate is influenced by the abundance of smelt. This relationship is shown in Figure 53.

3.6 Growth

Growth is a very important aspect when monitoring and analyzing fish populations (Ricker 1975). A number of models attempt to reliably predict individual fish growth in size (von Bertalanffy 1938, Knight 1969). In these models, size is some function of past size and growth. Food availability, latitude (temperature), and density of fish are thought to be some of the factors that influence fish growth. However, many of these models often do not consider factors responsible for the change in growth and none were found which considered the impact of hydroelectric development on fish growth.

Growth was not included in the model framework for a variety of reasons. How hydroelectric development affects fish growth is a very complex subject which deserves continued attention. In addition, information on the factors that affect fish growth (i.e., food availability) are limited from the Limestone reservoir, making a relationship

between food availability and growth difficult to develop. The objective of this model was to provide an idea of how reservoir operations affect fish abundance. To model the impact of hydroelectric development on fish growth is a subject which requires further attention. Fish growth in hydroelectric reservoirs has received little study in northern Canadian reservoirs.

Reservoir operations and impoundment impact fish growth by impacting the availability of food. A few studies were found in which growth was found to have changed following impoundment. For example, Deslandes et al. (1994) found that juvenile and adult longnose sucker and whitefish in fact showed sharp increases in their growth rate and condition factor following impoundment.

In Limestone, no change in growth was evident following impoundment. Condition factor (a measure of fish robustness) allows for a quantitative comparison of the condition of fish within a population, or between fish from different localities. In the Limestone reservoir, condition factors of fish have remained relatively unchanged since impoundment. These data influenced the inclusion of growth in the model, since it appeared that fish were similar in condition prior to and following impoundment. How fish growth has been impacted in a variety of reservoirs throughout Canada should be considered a topic for future research.

In other models, fish mortality rate is related to size, size is often related to growth, which is related to food availability (Cushing 1974). In these models, increased growth may result in increased fecundity, for example, which results in an increase in numbers to a fish population. Therefore, because growth was not considered in this model, an implicit relationship was used, that fish mortality was related to food availability.

Basically, an increased availability of food resulted in a direct effect on the mortality rate, a simplification from other models.

3.7 Summary

The framework for this computer simulation model is simple enough to handle cases where no age, sex or period-specific factors are desired, and flexible enough to handle a rather complex that may have more available data. The model framework is similar for all fish species. It provides the capability to easily change model inputs and relationships. The model is a simplification of the natural ecosystem, but encompasses the important factors to that must be considered when assessing potential impacts to fish resulting from a hydroelectric project. By understanding the factors that influence the different phases that influence fish life history we are gaining important insights into the population dynamics and improving our ability to predict and manage fish community dynamics in a changing ecosystem.

The importance of this application must be restated. First it fills an important gap in fisheries models that have not yet been applied to a hydroelectric reservoir. For example, density independent factors such as water level fluctuations caused by reservoir releases, often influence year class strength, and stock recruitment relationships. These density independent effects often obscure density-dependant stock-recruit relationships (Cushing 1988) making the application of density-dependant stock recruitment relationships to hydroelectric systems inappropriate. Also, this type of model allows the concerns of all different parties to be investigated through its use. For example, the interests of biologists, engineers and developers can be investigated by running alternative simulations. In this way it becomes an important tool for the decision making process.

4.0 Model Verification and Results

This chapter describes the model verification process and presents the results of the **HYDRAULIC** and **FISH** simulation models. Model verification is important to assure that model behaviour is comparable to the real-world system. Following the confirmation that the models represent the system under historical conditions, different operating strategies were tested through model simulations. The verification and results of each model are discussed separately below.

4.1 **HYDRAULIC** - model verification

The verification process for the **HYDRAULIC** model involved inputting historical hourly discharge rates from the Long Spruce and Limestone reservoirs. Once this was completed simulations were run and the results (i.e., water level fluctuations and average velocities in each reservoir region) were compared to the measured water levels and water velocities in the Limestone reservoir that corresponded with the inputted water level and discharge rates. After many trials, comparisons revealed that model results were consistent with measured values. Due to the large amount of data necessary to provide a comparison, these data were not included in this thesis.

4.1.1 Historical operating strategy

The historical discharge strategy that has been used in the Limestone reservoir has been described as a pulse release strategy, where high discharge rates correspond with times of high power demand. How the historical hourly discharge rate affects water levels in the upper reservoir region is shown graphically in Figure 54. Maximum water level fluctuations were calculated to be 1.83 m in the upper reservoir region; 1.61 in the middle reservoir region; and 1.40 m in the lower reservoir region (Table 1). An example

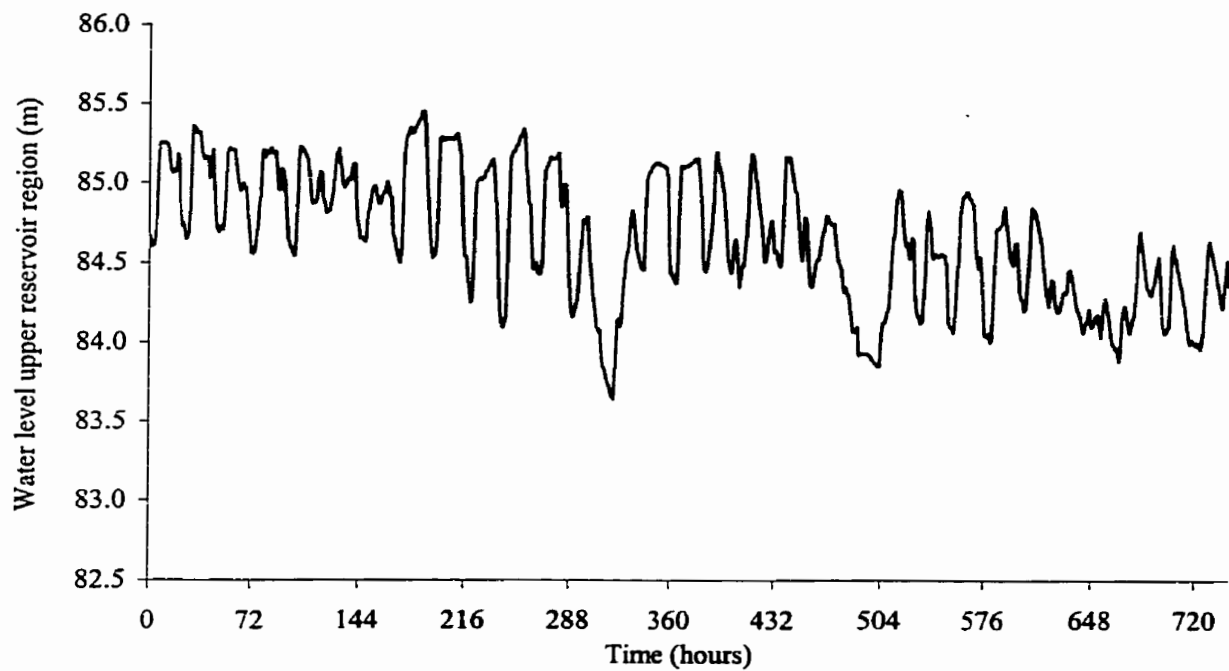


Figure 54. Water levels in the upper reservoir region that result from the historical operating strategy.

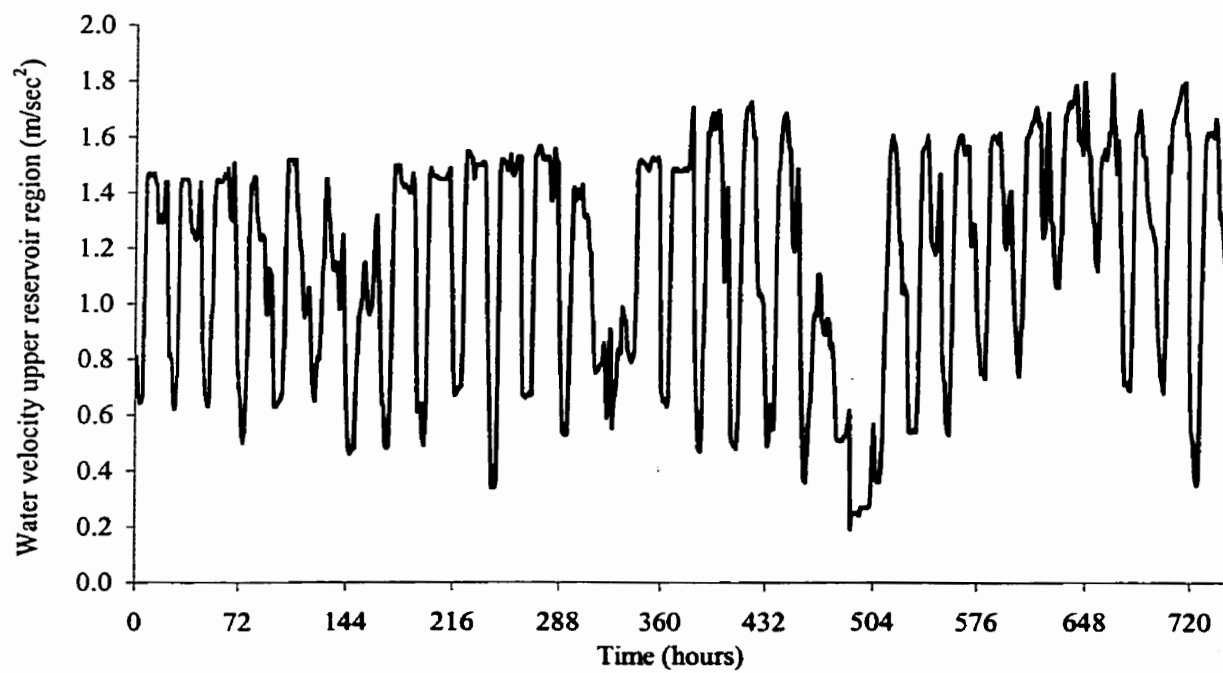


Figure 55. Water velocities in the upper reservoir region that result from the historical operating strategy.

Table 1. Water level fluctuations and average velocities for the three cross-sectional areas in the Limestone reservoir, in relation to the hourly discharge strategy.

Discharge strategy	Water level fluctuations			Average Water Velocity		
	(Upper)	(Middle)	(Lower)	(Upper)	(Middle)	(Lower)
	(m)			(m/sec)		
Historical Operation	1.83	1.62	1.41	1.14	0.21	0.16
Extreme Operation	2.92	2.65	2.38	1.2	0.23	0.17
Stable Operation	0.00	0.00	0.00	1.10	0.21	0.16
Winter Operation	1.17	1.00	0.83	1.34	0.26	0.21

of how water velocity changes over a one month period in the upper reservoir region is shown in Figure 55. Average velocities were calculated at 1.14 m/sec in the upper, 0.21 m/sec in the middle and 0.16 m/sec in the lower reservoir region (Table 1).

4.1.2 Extreme operating strategy

In comparison with the historical operating strategy, water level fluctuations with the extreme operating strategy were approximately 1 m greater in magnitude (Table 1). Figure 56 provides the water level change that occurs in the upper region of the Limestone reservoir with this operating strategy. Maximum water level fluctuations of 2.92 m were observed in the upper reservoir region, 2.65 m in the middle reservoir region and 2.38 m in the lower reservoir region (Table 1). Average water velocities were similar to those observed with the historical operating strategy at 1.2 m/sec, 0.23 m/sec and 0.17 m/sec for the upper, middle and lower reservoir regions, respectively (Table 1). Figure 57 provides the water velocities that occur in the upper reservoir region over a one month period.

4.1.3 Stable operating strategy

Maintaining a constant discharge rate from both the Long Spruce and Limestone generating stations over a one month period results in stable water levels and average velocities (Figure 58 and 59). The discharge rate for this simulation was held constant at 3075 m³ per second, which resulted in average water velocities of 1.1 m/sec, 0.21 m/sec and 0.16 m/sec in the upper, middle and lower reservoir regions, respectively.

4.1.4 Winter operating strategy

Maximum water level fluctuations were 1.17 m in the upper reservoir region; 1 m in the middle reservoir region; and 0.83 m in the lower reservoir region with the winter

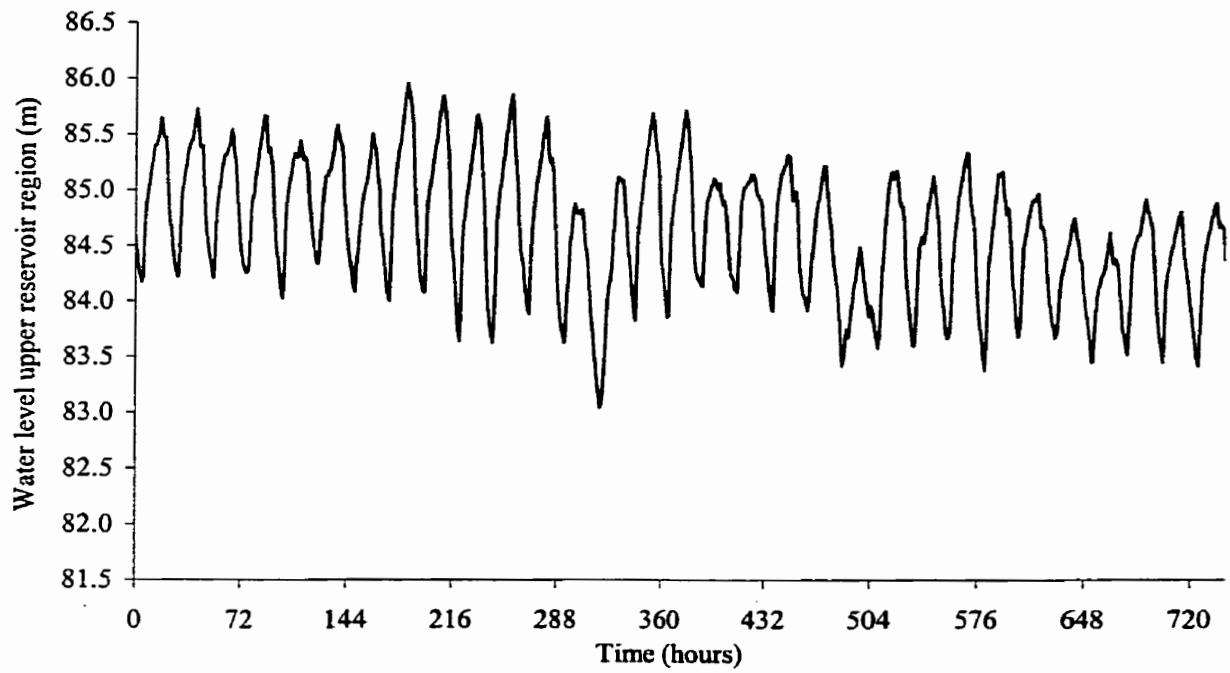


Figure 56. Water levels in the upper reservoir region that result from the extreme operating strategy.

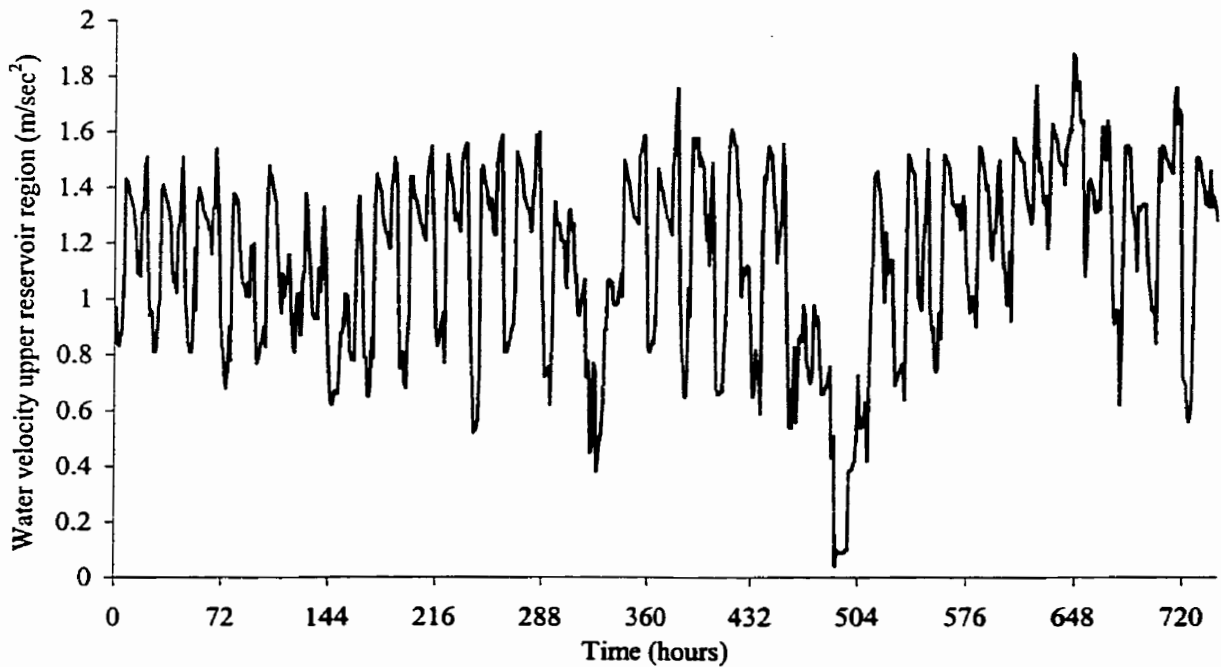


Figure 57. Water velocities in the upper reservoir region that result from the extreme operating strategy.

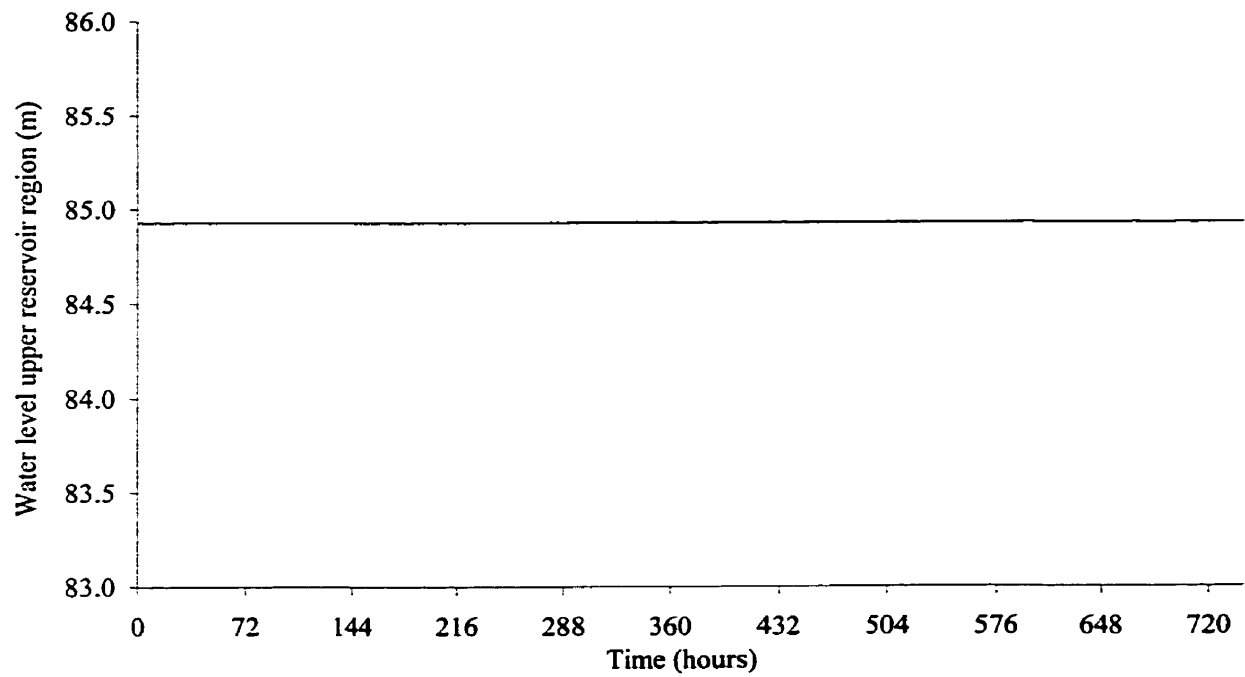


Figure 58. Water levels in the upper reservoir region that result from the stable operating strategy.

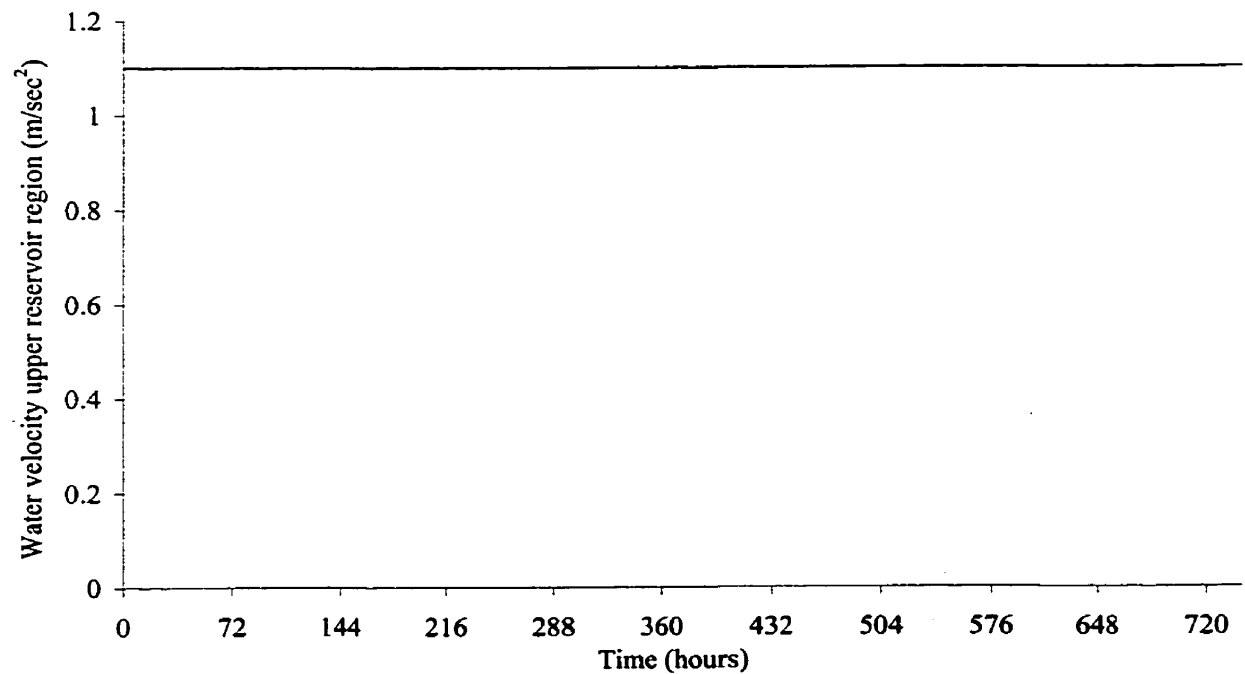


Figure 59. Water level in the upper reservoir region that result from the stable operating strategy.

operating strategy (Table 1). Figure 60 shows the water level change in the upper reservoir region over a one month time period. In comparison with the other operating strategies, maximum water level fluctuations were smaller in magnitude despite the larger total volume of water discharge over a one month period. This was because the hourly discharge rates from the Limestone and Long Spruce generating stations, corresponding with similar time intervals, were relatively similar. However, because the discharge rate was on average higher than other strategies investigated, average water velocities were the higher at 1.34 m/sec, 0.26 m/sec and 0.21 m/sec in the upper, middle and lower reservoir regions, respectively (Table 1). Figure 61 provides the water velocities that occurred in the upper reservoir region using this discharge strategy.

4.2 FISH

As previously discussed, this thesis analyzed 12 combinations of discharge strategies. The combinations of monthly and hourly discharge strategies used during each simulation are presented in Table 2. Table 2 is also provided in the folder in the back of this thesis for reference when examining the results of each simulation.

4.2.1 Scenario 1 – Model verification

Scenario 1 was used to verify the **FISH** model. This scenario used historical discharge data (i.e., the current operating strategy) from the Long Spruce and Limestone generating stations for the entire 25 year simulation period. Similarities between trends in fish population data from the Limestone and Long Spruce reservoirs, and those predicted by model simulations, would suggest that the model was working to describe the real-world environment. In order to compare model results to fisheries survey data from the Long Spruce and Limestone reservoirs, Tables 3 and 4, respectively were

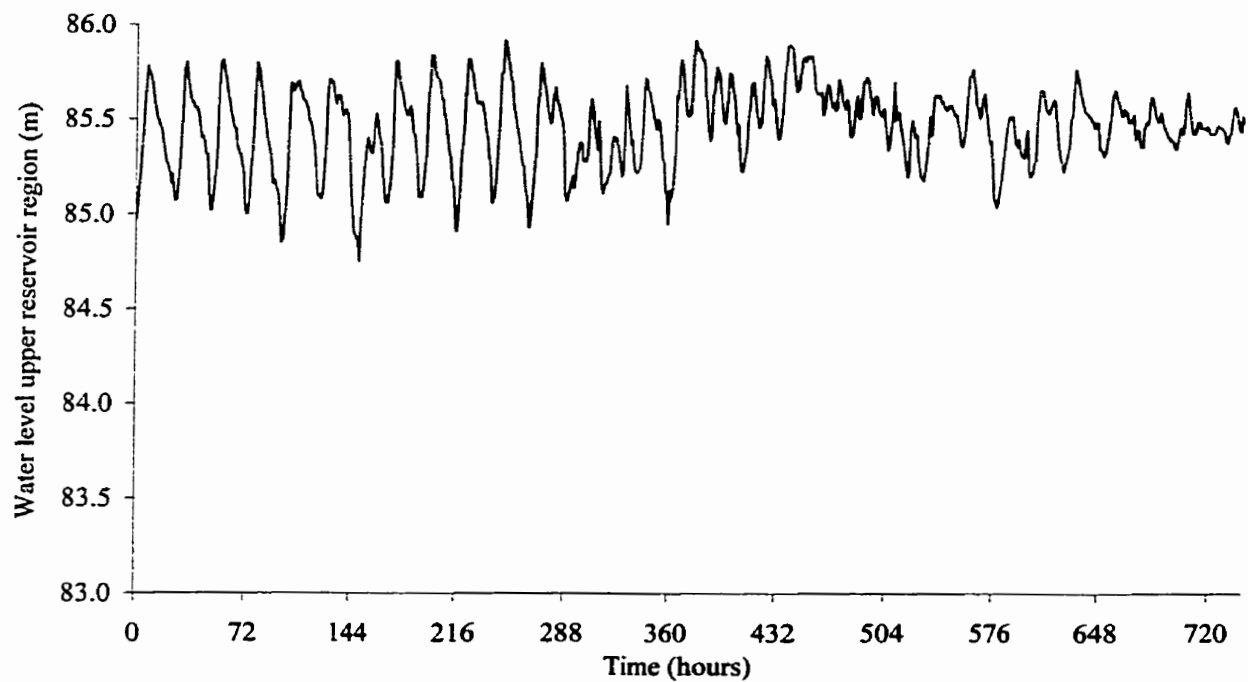


Figure 60. Water level in the upper reservoir region that result from the winter operating strategy.

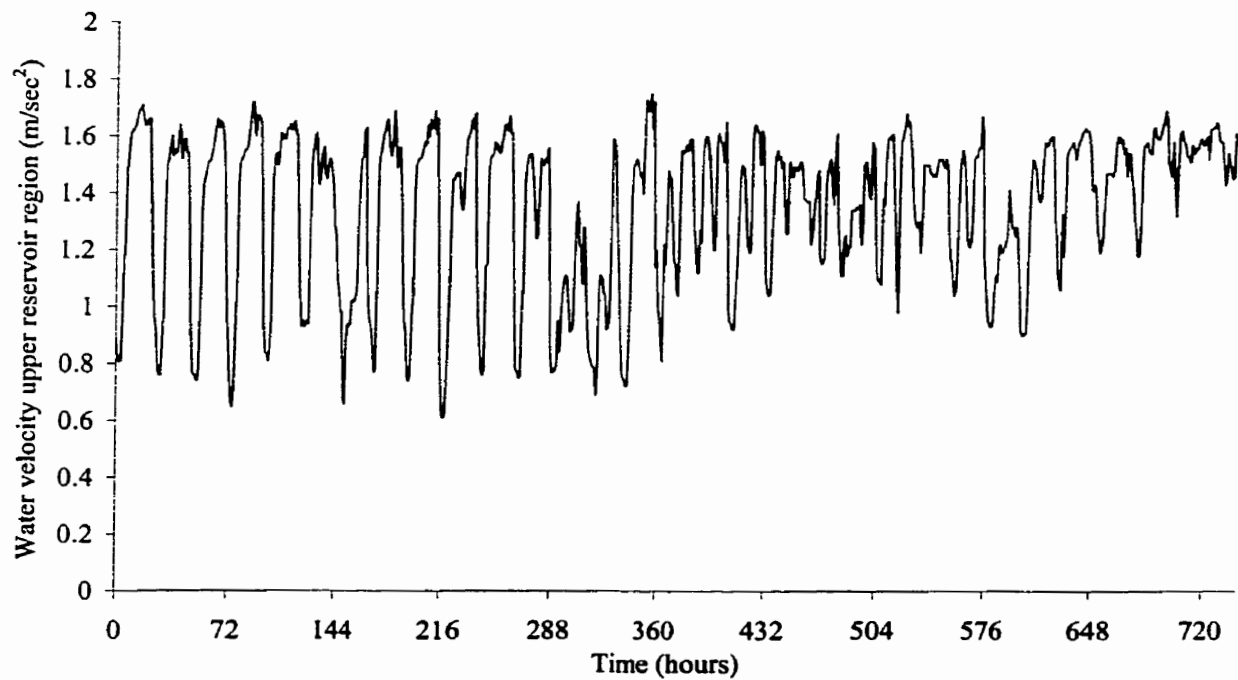


Figure 61. Water velocities in the upper reservoir region that result from the winter operating strategy.

Table 2. The alternative combination of monthly and hourly operating strategies investigated by the **FISH** model.

Scenario	Seasonal operating strategy		Hourly operating strategy			
			Spring	Summer	Fall	Winter
Scenario 1	Historical		Historical	Historical	Historical	Historical
Scenario 2	Historical		Extreme	Extreme	Extreme	Extreme
Scenario 3	Historical		Stable	Stable	Stable	Stable
Scenario 4	Historical		Winter	Winter	Winter	Winter
Scenario 5	Spring Flood		Historical	Historical	Historical	Historical
Scenario 6	Spring Flood		Extreme	Extreme	Extreme	Extreme
Scenario 7	Spring Flood		Stable	Stable	Stable	Stable
Scenario 8	Spring Flood		Winter	Winter	Winter	Winter
Alternative 1	Historical		Stable	Historical	Winter	Winter
Alternative 2	Historical		Historical	Historical	Stable	Stable
Alternative 3	Historical		Stable/Historical	Winter	Winter	Winter
Smelt	Historical		Historical	Historical	Historical	Historical

Table 3. The number of northern pike, lake whitefish, longnose sucker and walleye captured during fisheries surveys of the Limestone reservoir.

Year	Northern pike	Lake whitefish	Longnose sucker	Walleye
1989	17	24	1495	0
1990	20	27	1364	13
1991	N/A	N/A	N/A	N/A
1992	98	19	255	54
1993	71	27	157	24
1994	33	27	292	25
1995	63	41	353	23
1996	36	22	201	21
1997	25	15	364	37
1998	37	15	343	78
1999	61	39	396	164

Table 4. The number of northern pike, lake whitefish, longnose sucker and walleye captured during fisheries surveys of the Long Spruce reservoir.

Year	Northern pike	Lake whitefish	Longnose sucker	Walleye
1989	116	122	19	56
1992	87	36	38	53
1993	75	23	167	32
1996	43	32	32	95
1999	71	18	64	199

provided which summarize the numbers of northern pike, lake whitefish, longnose sucker, and walleye captured in each reservoir since monitoring was initiated.

Northern pike

The model simulation that used historical discharges suggested that shortly after impoundment, northern pike populations increased, but that as the reservoir aged, their population decreased gradually over time. A large increase in northern pike abundance was observed in year four of the simulation (Figure 62), which was followed by a gradual decrease to 22,811 individuals by the end of the 25 year simulation (Table 5).

The trend in northern pike abundance predicted by the results of this simulation were consistent with trends that have been observed in other reservoirs. Chapter 2 discussed that northern pike populations in many reservoirs increase dramatically in the first few years following reservoir development. Biologists have attributed the initial increase in abundance to newly flooded vegetation which is thought to provide important spawning and nursery habitat for the development of young northern pike. However, once water levels stabilize in a reservoir (as seen in Limestone 5 years after reservoir development), northern pike populations have been found to decrease gradually with time. The results provided in Figure 62 describe this general trend.

The Scenario 1 results for northern pike were also comparable to fisheries survey data from the Limestone reservoir. In Limestone, fisheries survey data suggested that the catch of northern pike was highest four years after impoundment (1992) and second highest five years after impoundment (1993) (Table 3). Also, since 1992, the number of northern pike captured during these surveys have decreased, suggesting that the northern pike population may be declining in the reservoir (Table 3).

Table 5. The number of northern pike, lake whitefish, longnose sucker and walleye that result from each discharge scenario investigated by the **FISH** model.

Discharge scenario	Northern pike	Lake Whitefish	Longnose sucker	Walleye
Scenario 1	22,811	5,713	24,707	74,482
Scenario 2	4,680	0	627	0
Scenario 3	55,191	89,742	47,876	67,779
Scenario 4	23,527	38,526	22,715	52,226
Scenario 5	91,520	3,656	10,835	66,423
Scenario 6	4,681	0	627	0
Scenario 7	99,342	72,947	31,472	63,216
Scenario 8	90,849	25,320	10,258	47,816
Alternative 1	39,194	42,474	14,959	69,340
Alternative 2	23,527	104,022	22,716	52,226
Alternative 3	37,728	43,722	13,402	69,480
Smelt 1	26,210	1,158	20,688	90,257

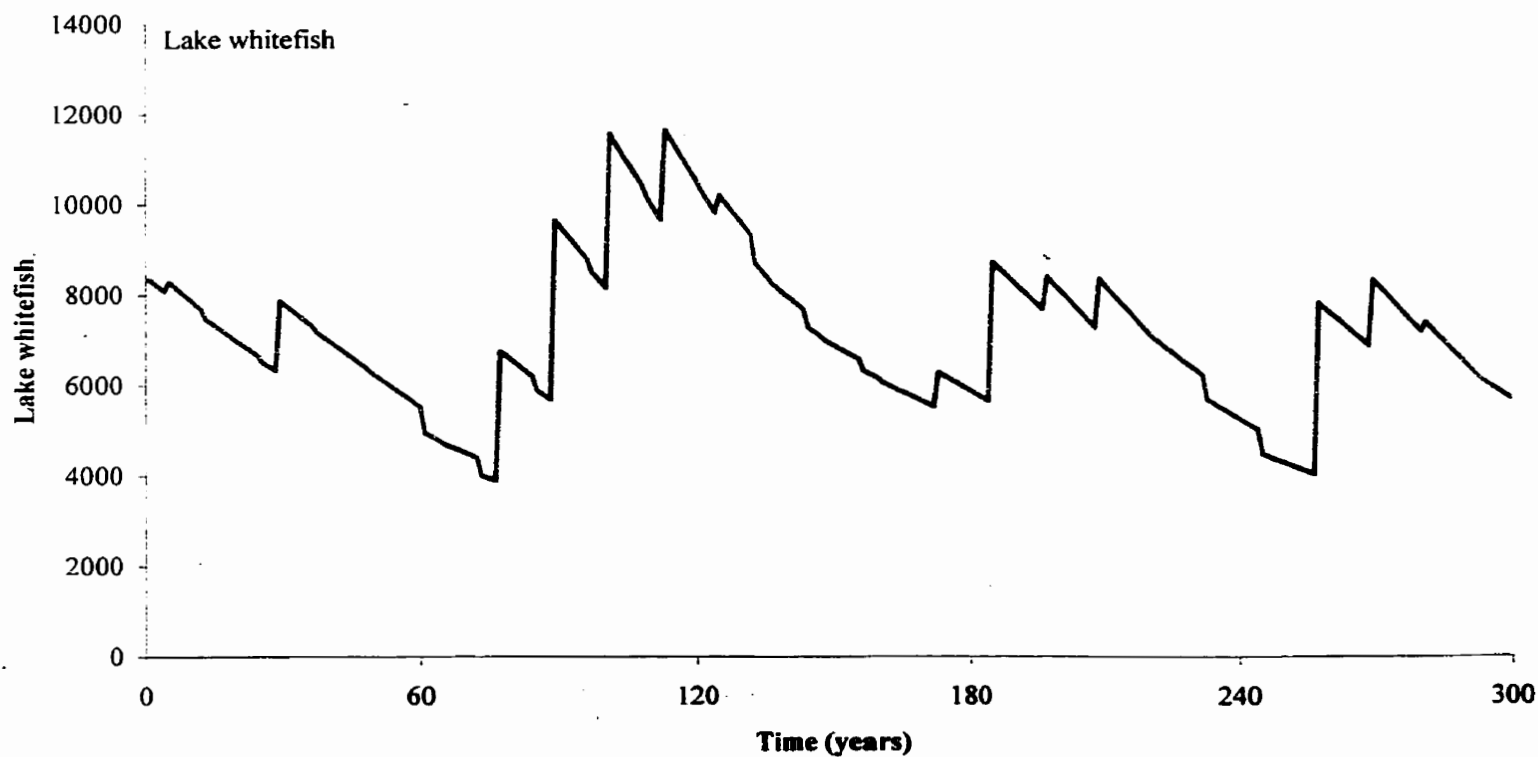
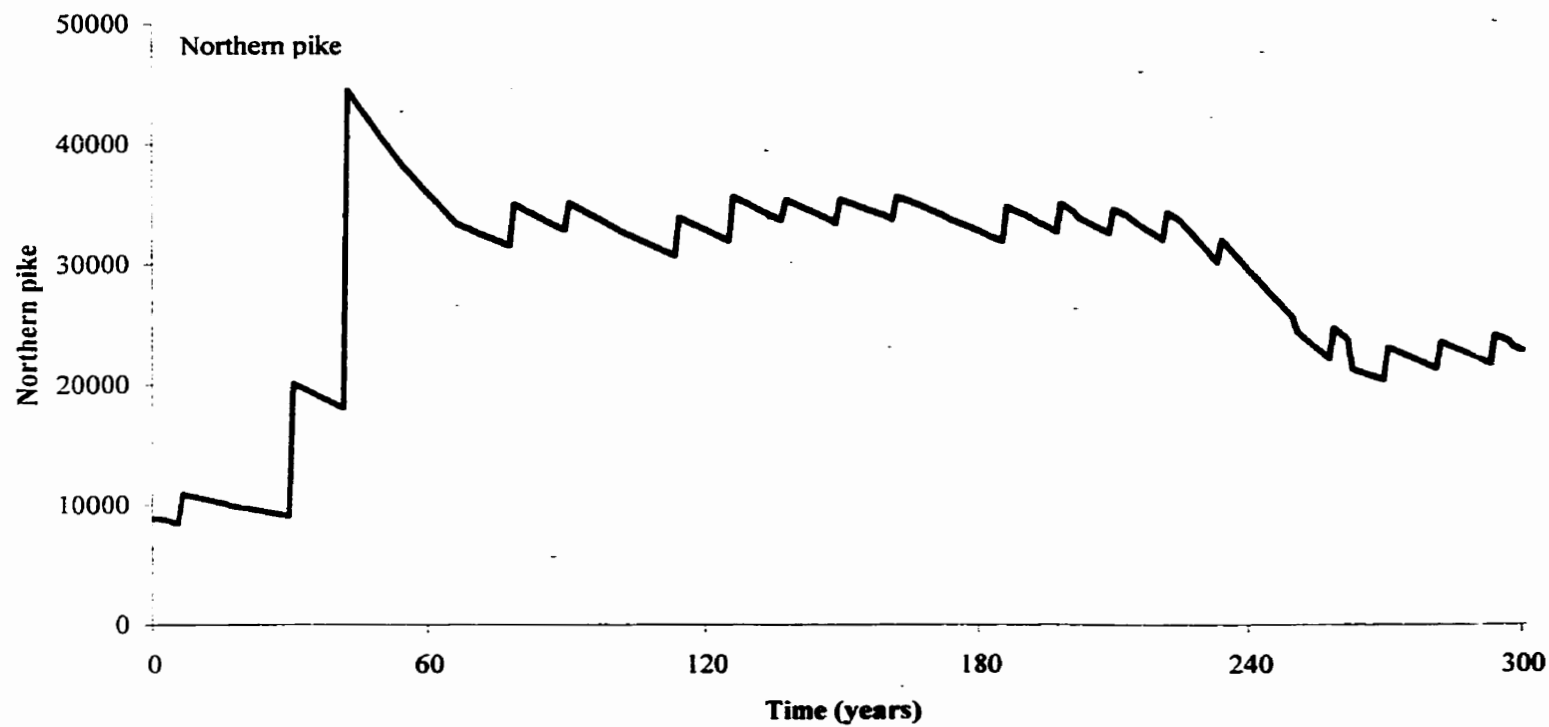
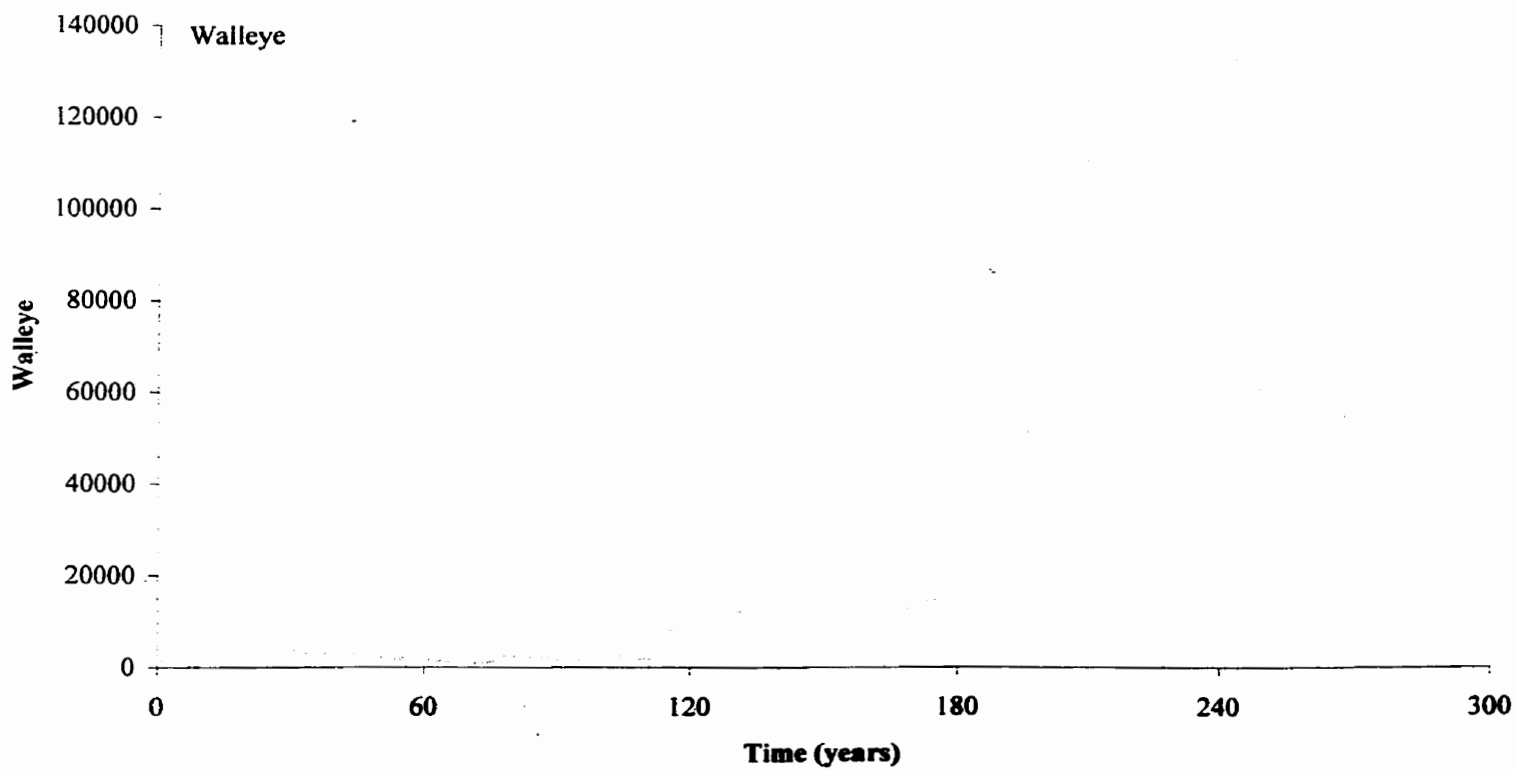
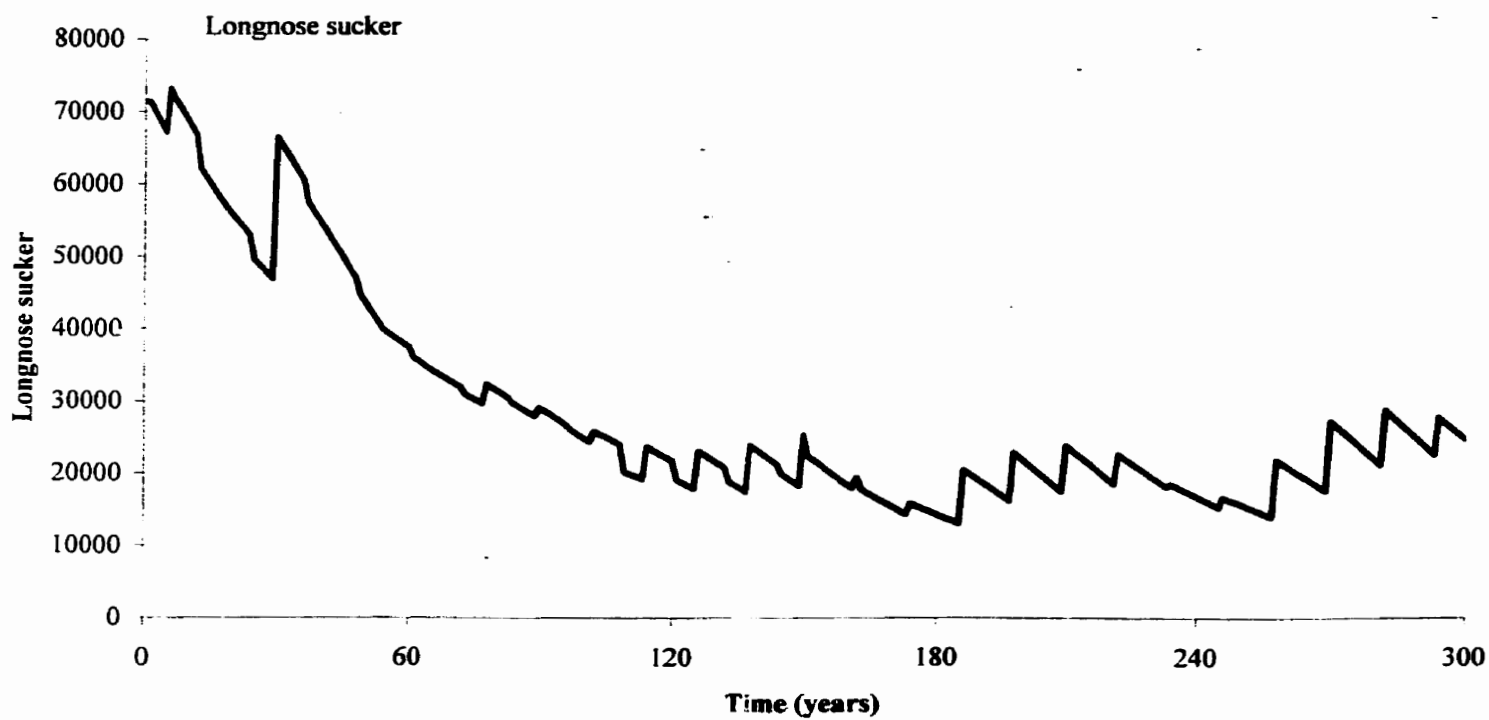


Figure 62. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario



ne Scenario 1 simulation.

Fisheries survey data from the Long Spruce reservoir also compares well with the northern pike results in Scenario 1. Fisheries surveys of the Long Spruce reservoir were initiated in 1989, 10 years after this reservoir was developed (Table 4). In the first year of the survey, catches of northern pike were highest, when the reservoir was 10 years old. Catches subsequently declined over time to approximately 20% of the 1989 catch in 1999. If we assume that northern pike populations in the Limestone reservoir follow the trend observed in the Long Spruce reservoir, then the prediction that northern pike populations will gradually decrease over time, is supported.

Lake whitefish

Model simulations using historical discharges suggested that recruitment to the lake whitefish population varies highly from year to year which results in the abundance of lake whitefish in the Limestone reservoir fluctuating over time (Figure 62). Figure 62 shows that lake whitefish abundance was highest 10 years after impoundment, and decreased to 5,713 individuals by the end of the simulation (Table 5). The results suggest that although their abundance varies in the reservoir over time, an overall decreasing trend in whitefish numbers was observed.

Chapter 2 discussed the trends that have been observed in lake whitefish populations in other reservoirs following river impoundment. The literature suggested that lake whitefish populations have been found to both increase and decrease. Also, it was suggested that lake whitefish populations may be influenced by a wide variety of physical and biological factors following impoundment, and that predicting the response of their population to reservoir development may be highly site specific. This makes it difficult to predict how lake whitefish populations may be affected by hydroelectric development.

The number of lake whitefish captured in fisheries surveys from 1989 – 1999 in the Limestone reservoir has varied from year to year, and no clear trend has become evident from data analyses (Table 3). Data from the Long Spruce reservoir suggested that the number of lake whitefish captured was highest in 1989 (the first year of the fisheries surveys) and decreased to approximately one-third of 1989 catches four years later in 1993 (Table 4). Although based on little data, it appears as though a decrease in lake whitefish populations may have occurred in the Long Spruce reservoir since 1989. If we assume that the lake whitefish population of the Limestone reservoir will follow the trend observed in the Long Spruce reservoir, then the decreasing trend predicted by the results of Scenario 1 is supported.

Modeling lake whitefish populations in reservoirs is difficult given the number of factors that influence their population following impoundment. This difficulty is compounded in a reservoir such as Limestone where a population trend has not become evident from the field data. Van Oosten and Hile (1992), in failing to find a correlation between meteorological-limnological conditions and the strength of whitefish year classes, commented that "the factors which determine the strength of year classes are so numerous and have such complex inter-relationships that it is not possible on the basis of present information to detect and evaluate the effect of any single one of them". Conceptually, in a reservoir such as Limestone, it could be predicted that whitefish spawning success might improve over time, due to decreased amounts of sediments in the water column (as the reservoir ages), a general decrease in predator abundance (i.e., pike) over time, and potential increased food abundance (i.e., potential increased invertebrate abundance) (Machniak 1975b). However, in the Limestone reservoir, it is still unclear

how invertebrate populations have been affected by impoundment, and the addition of smelt and short-term water level fluctuations may add additional factors that could be adversely affecting lake whitefish populations. Further study is needed to identify the potential factors affecting whitefish populations in hydroelectric reservoirs and more specifically the Limestone reservoir.

Longnose sucker

Model simulations using historical discharges suggested that little or no recruitment occurred to the longnose sucker population for the first 10 years after development of the Limestone reservoir (Figure 62). Due to this lack of recruitment, the longnose sucker population decreased to approximately 20% of their initial numbers 15 years after reservoir development. However, after 15 years, the longnose sucker population stabilized, and increased to 24,707 individuals, approximately 25% of their initial numbers by the end of the 25 year simulation (Table 5). The decreasing trend predicted by the model may be explained by water level fluctuations during spawning time which negatively affect egg survival, and the initial increase in the northern pike population. As the reservoir ages, northern pike populations tend to decrease, which may account for the stabilization and slight increase in the longnose sucker abundance 15 years after reservoir development (Figure 62).

Fisheries data from the Limestone reservoir supports the decreasing trend described by the results of Scenario 1. Longnose sucker have comprised the majority of the fish catch in the Limestone reservoir since 1989. However, although the numbers of longnose sucker captured during fisheries surveys has not decreased, most of the longnose sucker captured are older, larger fish recruited to the population prior to the development of the

Limestone reservoir (Bretecher and MacDonell 2000). Bretecher and MacDonell (1997) stated that once these older age classes disappear from the population, that the abundance of longnose sucker in the Limestone reservoir may be substantially reduced.

Adding further support to the decreasing trend described by Scenario 1 results are fisheries survey data from the Long Spruce reservoir. These data support the hypothesis that reservoir development negatively influences recruitment to the longnose sucker population. In the Long Spruce reservoir, longnose sucker comprise a much smaller proportion of the fish catch when compared with the catch from the Limestone reservoir. Bretecher and MacDonell (1998) hypothesize that older year classes of longnose sucker have already disappeared from the Long Spruce reservoir, thus explaining the relatively small proportion of the catch. If we assume that the longnose sucker population in the Limestone reservoir will evolve to resemble that of the Long Spruce reservoir, then the results accurately describe this trend.

Walleye

Results of Scenario 1 show that the abundance of walleye increased to approximately 15 times their initial abundance, 15 years after development of the Limestone reservoir (Figure 62). After the fifteenth year of the simulation, the walleye population rapidly increased in abundance, peaked and subsequently decreased to 74,482 individuals by the end of the simulation (Table 5). Results suggest a dramatic increase in walleye numbers following reservoir development.

Chapter 2 discussed the general trend in walleye populations observed in other reservoirs following impoundment. The literature suggested that walleye populations increase in abundance as the reservoir ages. A number of factors are thought to

positively influence walleye populations in reservoirs. For example, scientific literature suggests that walleye may not be as susceptible to water level fluctuations as other fish species. This is because walleye can spawn at sufficient depths to avoid the adverse impacts of fluctuating water levels. Also, it is thought that wave-washing which exposes gravel substrates as a reservoir ages improves walleye spawning success over time (Machniak 1975c, Bennet and MacArthur 1990). The addition of smelt to the Limestone reservoir may also have a positive impact on walleye populations by providing an abundant food source. Finally, a decrease in northern pike abundance as the reservoir ages reduces the amount of predation.

The increase in walleye numbers that resulted from Scenario 1 was supported by fisheries survey data from the Limestone reservoir. In 1989, walleye were absent from fisheries surveys of the Limestone reservoir. By 1999, walleye were the second most abundant fish species captured ($n=164$) (Table 3). These data indicate large increases in walleye numbers in the Limestone reservoir 10 years after impoundment. Similarly, data from the Long Spruce reservoir suggest that walleye have steadily increased since monitoring began in 1989. A total of 56 walleye were captured in 1989. Ten years later, 199 walleye were captured, an increase of nearly 400%. This made walleye the most abundant fish species captured in this reservoir (20 years after impoundment) (Table 4).

4.2.1.1 Summary

The trends observed in results of Scenario 1 for each fish species were supported by the scientific literature and fisheries survey data from the Limestone and Long Spruce reservoirs. Because this simulation represented the historical conditions in the Limestone reservoir, these results were used to compare with results of other simulations. Higher

abundances of fish relative to this strategy would indicate the success of that strategy to improve conditions for that fish species in the reservoir. To facilitate a comparison, the results of the historical discharge strategy (Figure 62) was included as a pull out at the back of the thesis.

4.2.2 Scenario 2 – (Historical and Extreme)

Results indicated that each fish population was adversely affected by this combination of discharge strategies. High water level fluctuations (over 2 m in each reservoir region) that result from the extreme operating strategy reduced the egg survival of each fish species (Figure 63). Lake whitefish and walleye numbers were reduced to zero, while northern pike and longnose sucker were 4,680 and 627 individuals, respectively, several orders of magnitude less than numbers observed with the Scenario 1 simulation. If this simulation were continued for a longer period of time, numbers of northern pike and longnose sucker would also reach zero. These results suggest that a reservoir operations strategy which increases short-term water level fluctuations adversely impacts each fish population included in the model.

4.2.3 Scenario 3 – (Historical and Stable)

The maintenance of stable discharge rates increased abundances of northern pike, lake whitefish, and longnose sucker, relative to Scenario 1. Northern pike numbers were approximately two times higher at 55,191 individuals (Table 5). Instead of gradually decreasing in number as the reservoir aged, (as observed in Scenario 1), their population increased over time with this scenario (Figure 64). Longnose sucker abundance decreased for approximately 10 years after reservoir development. However, after this 10 year period, longnose sucker abundance began to increase over time until the end of the

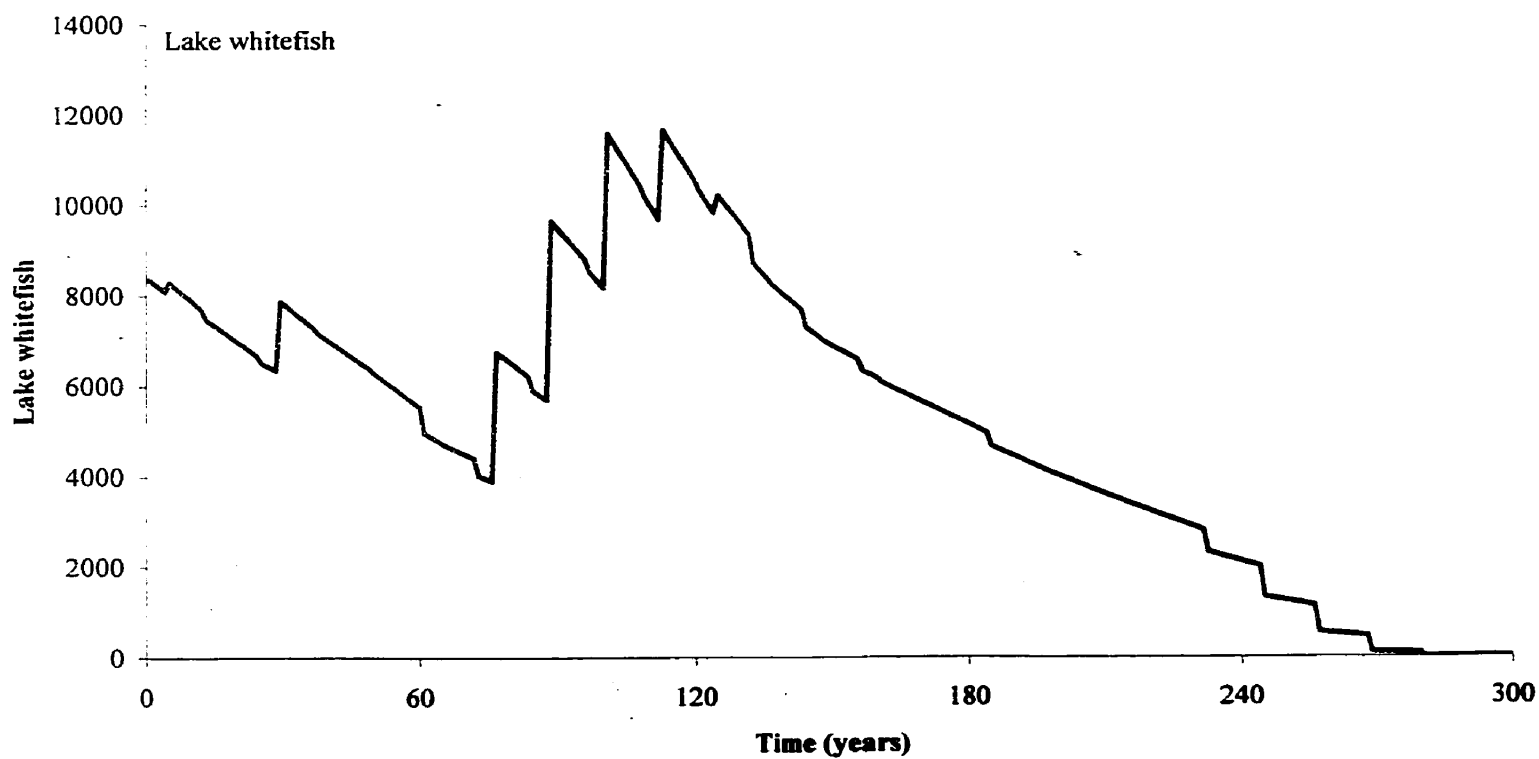
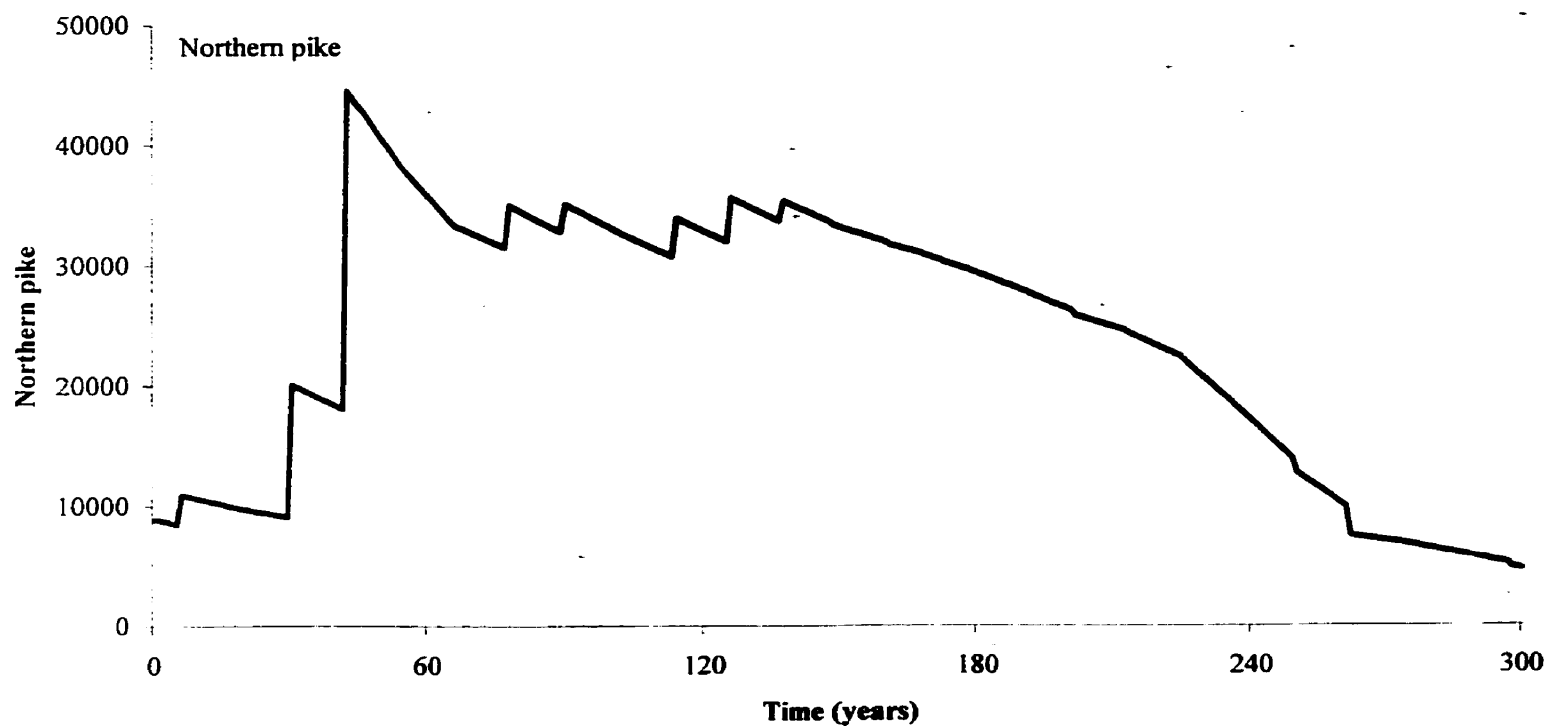
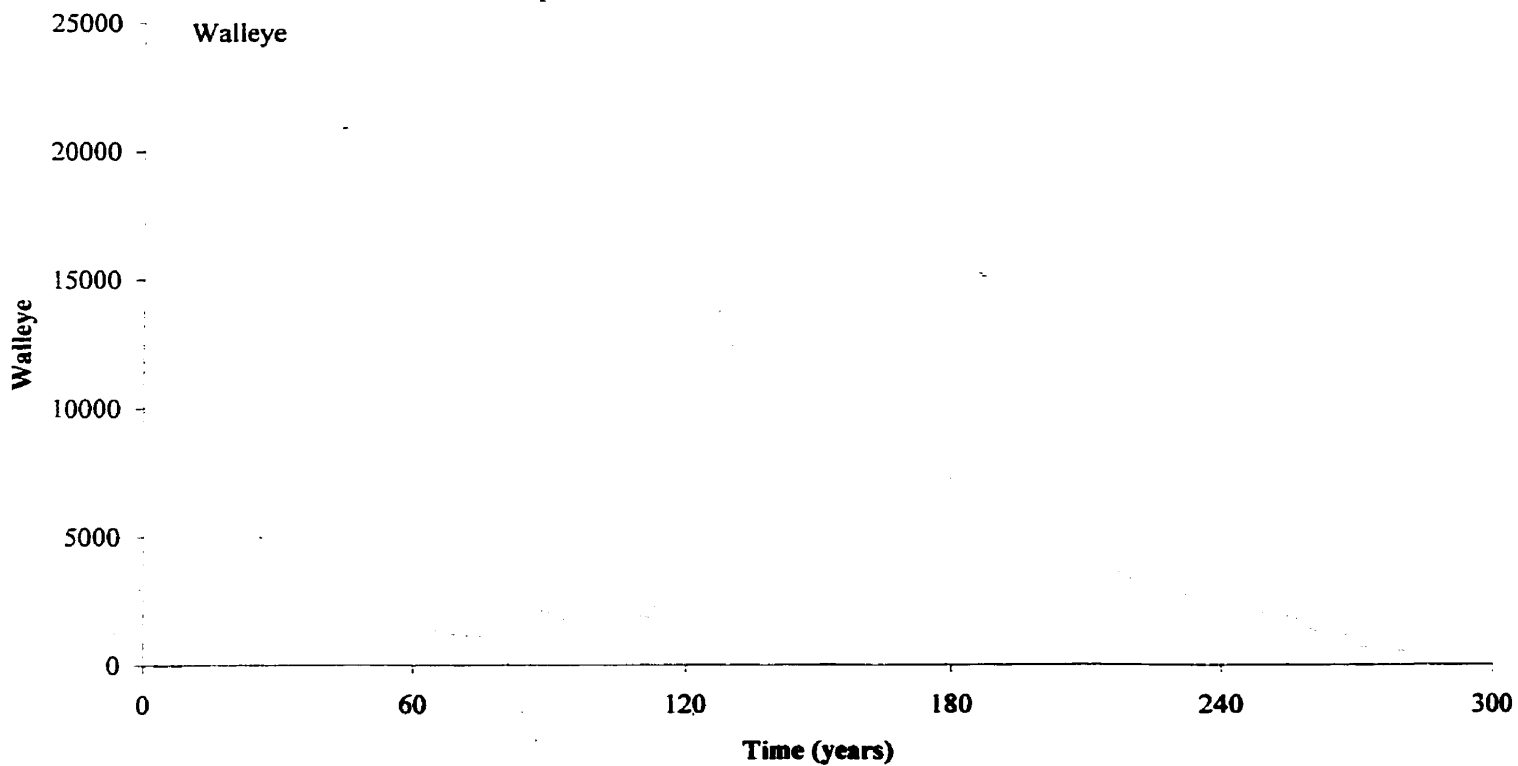
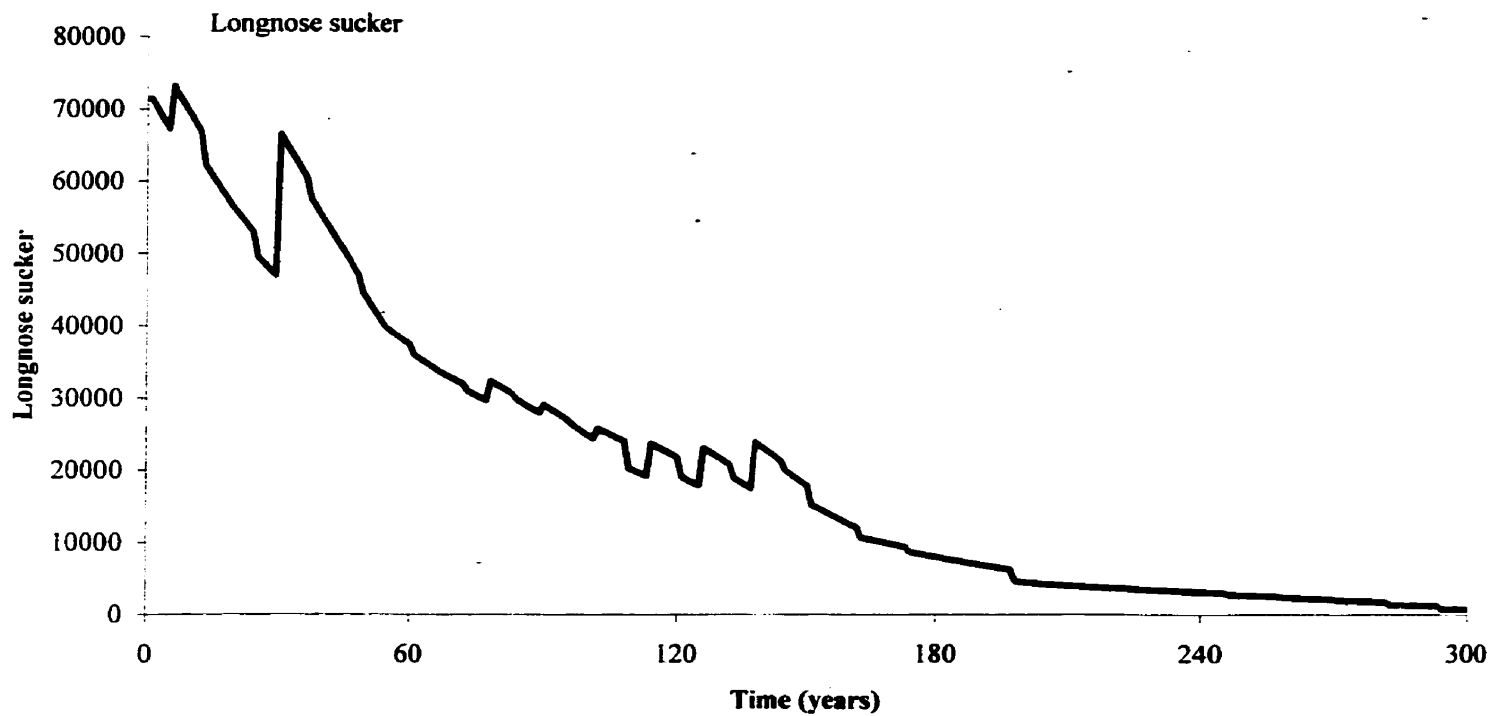


Figure 63. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario



the Scenario 2 simulation.

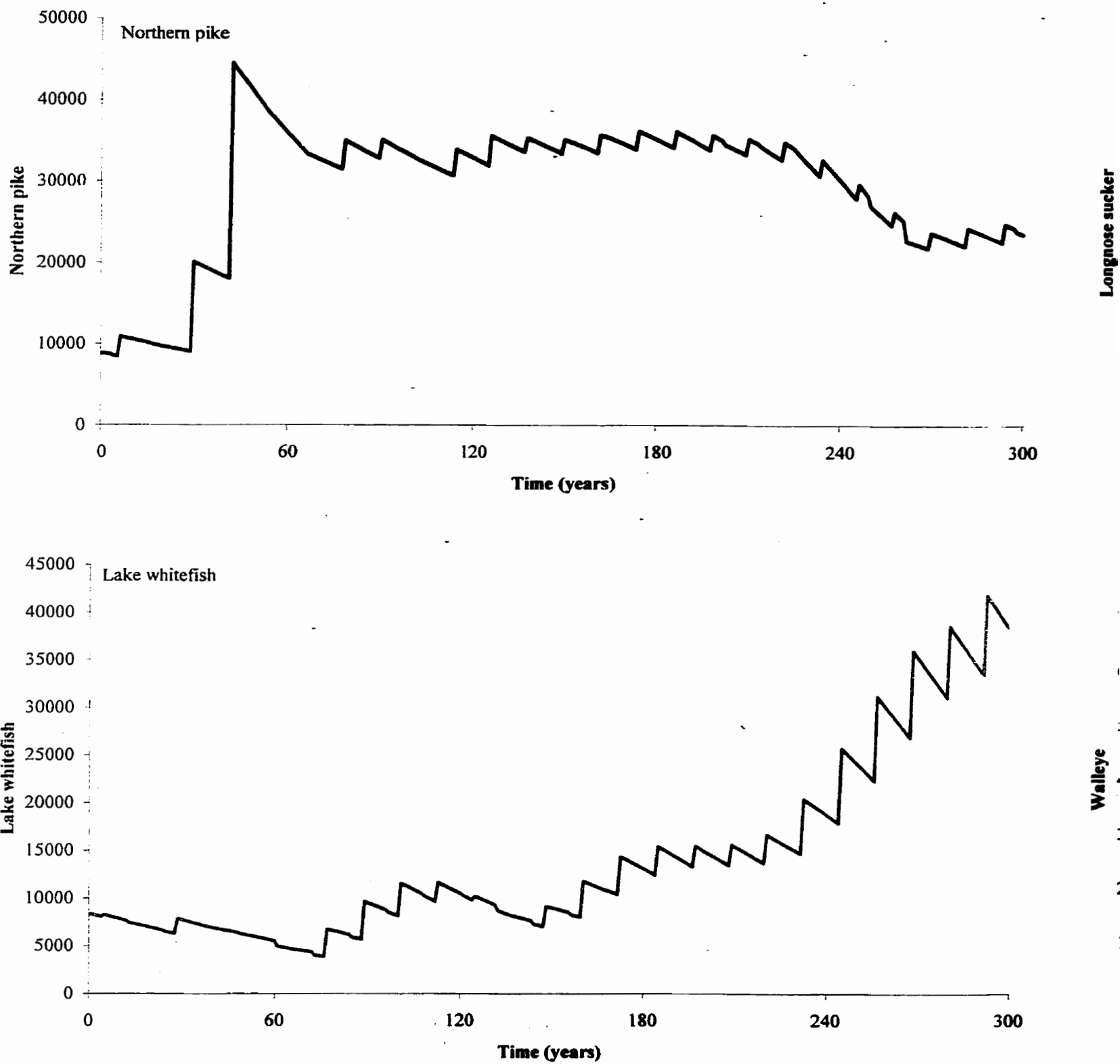
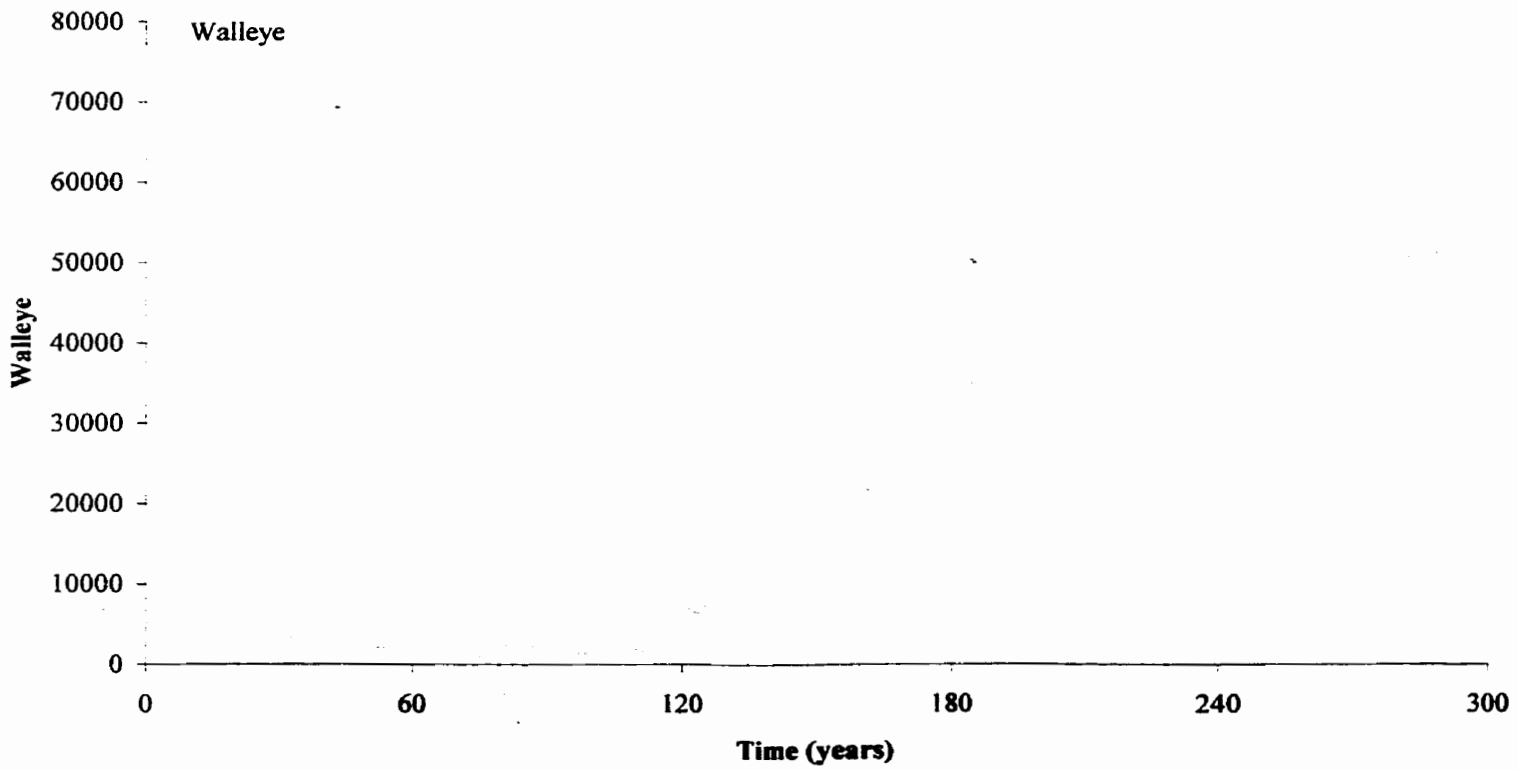
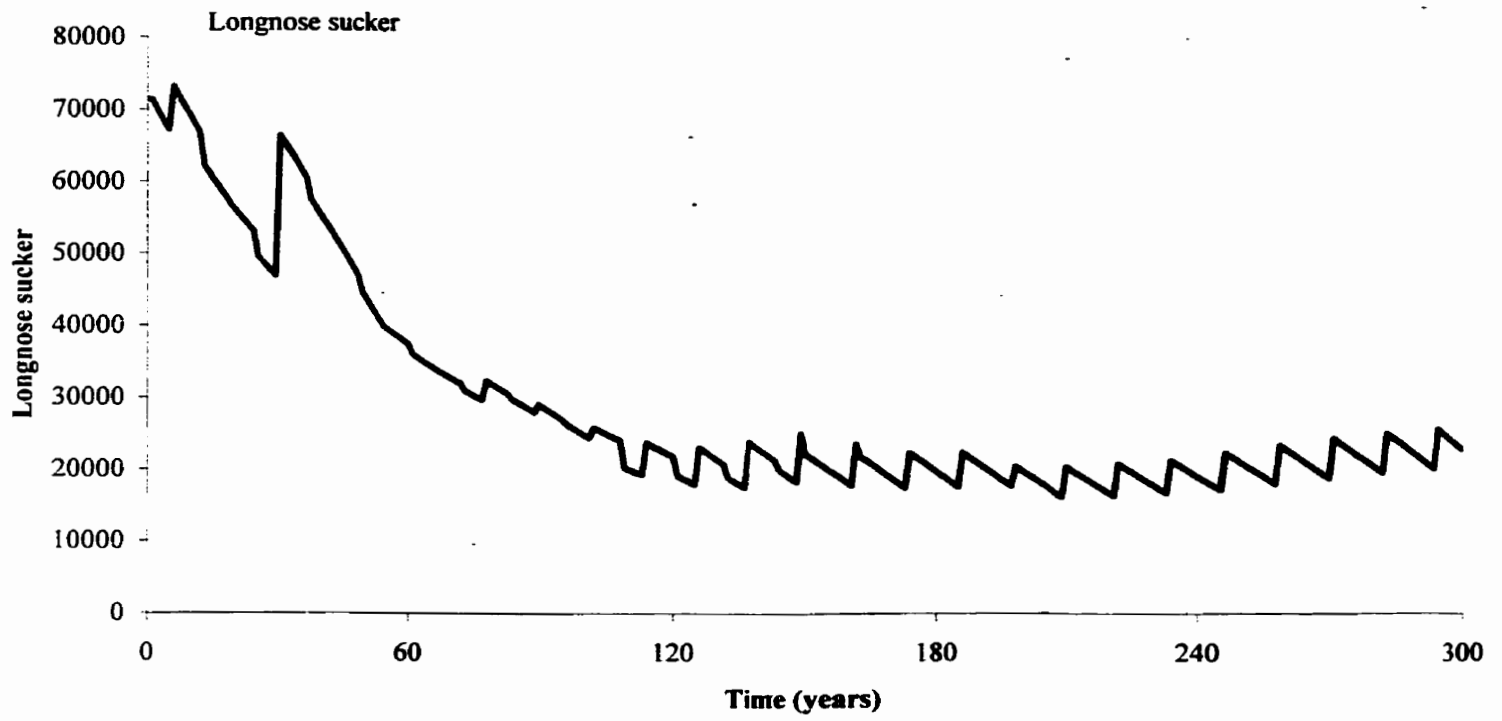


Figure 64. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario 3 s



the Scenario 3 simulation.

25 year simulation (Figure 64). Of all the Scenarios analyzed in this thesis, this combination of discharge strategies produced the highest number of longnose sucker, (47,876) (Table 5), approximately two times higher than numbers with Scenario 1. Lake whitefish numbers were approximately 15 times higher when compared with Scenario 1, at 89,742 (Table 5). Instead of gradually decreasing over time (the trend observed Scenario 1), an increasing trend in lake whitefish numbers was observed (Figure 64). The abundance of walleye increased significantly over the 25 year simulation period, however, their numbers were lower when compared to Scenario 1, at 67,779 (Table 5). The reason that walleye numbers were lower than Scenario 1 is due to a more rapid increase in walleye abundance, which subsequently resulted in a high rate of cannibalism earlier on in the simulation (Figure 64). The results of this simulation indicated that the maintenance of stable water levels in a reservoir would benefit each fish species included in the model.

4.2.4 Scenario 4 – (Historical and Winter)

The abundances and trends observed for northern pike and longnose sucker populations with Scenario 4 were similar to the those observed with Scenario 1 (Figure 65). Northern pike increased in abundance four years after impoundment and gradually decreased as the reservoir aged to 23,527 individuals (Table 5). The abundance of longnose sucker decreased for a 10 year period following reservoir development. After this 10 year period, longnose sucker abundance remained relatively stable for the remainder of the 25 year simulation period (Figure 65). Their numbers were found to be slightly lower when compared with Scenario 1 at 22,715 individuals. Lake whitefish abundance increased significantly with the Scenario 4 simulation (Figure 65). Their

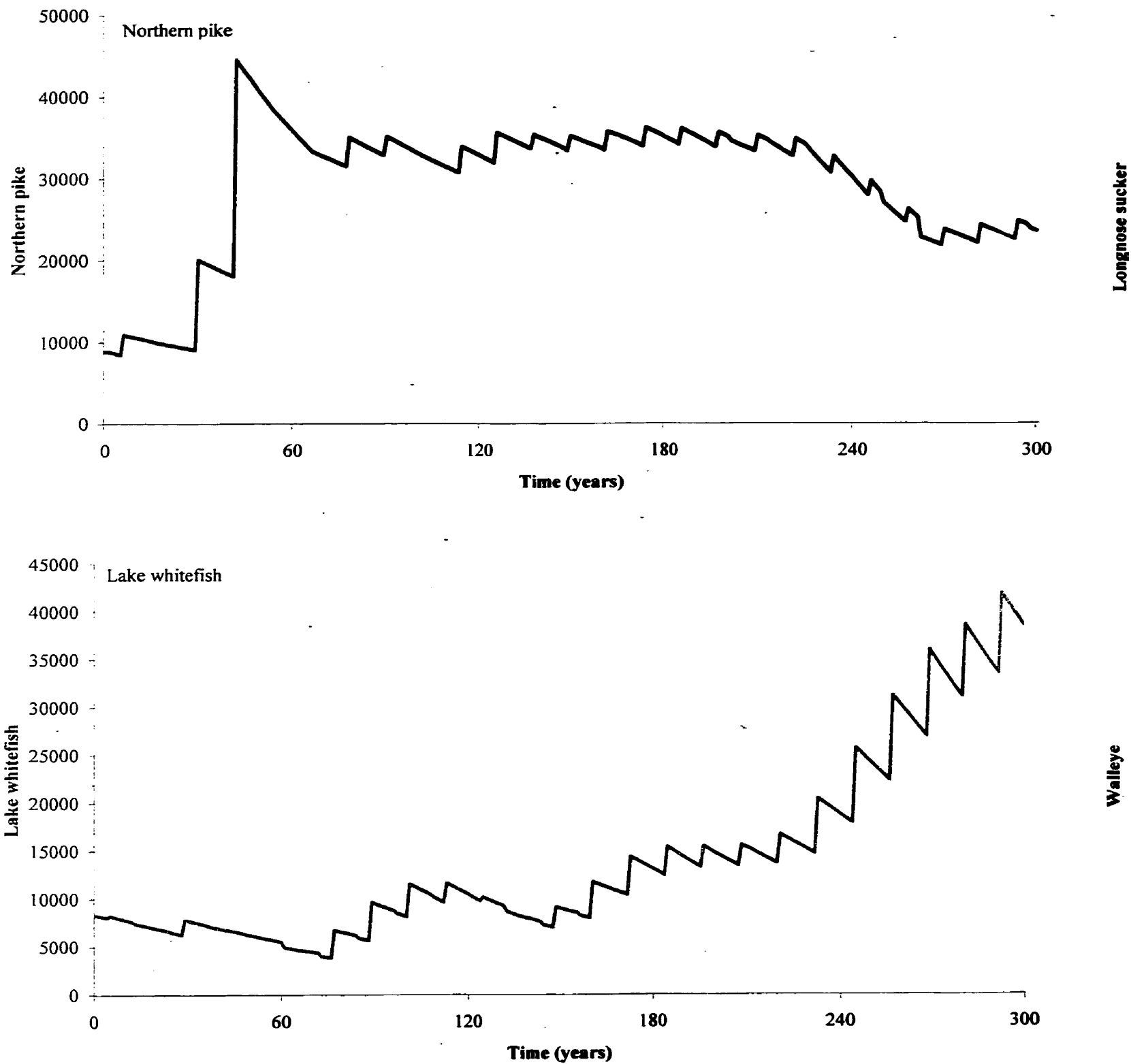
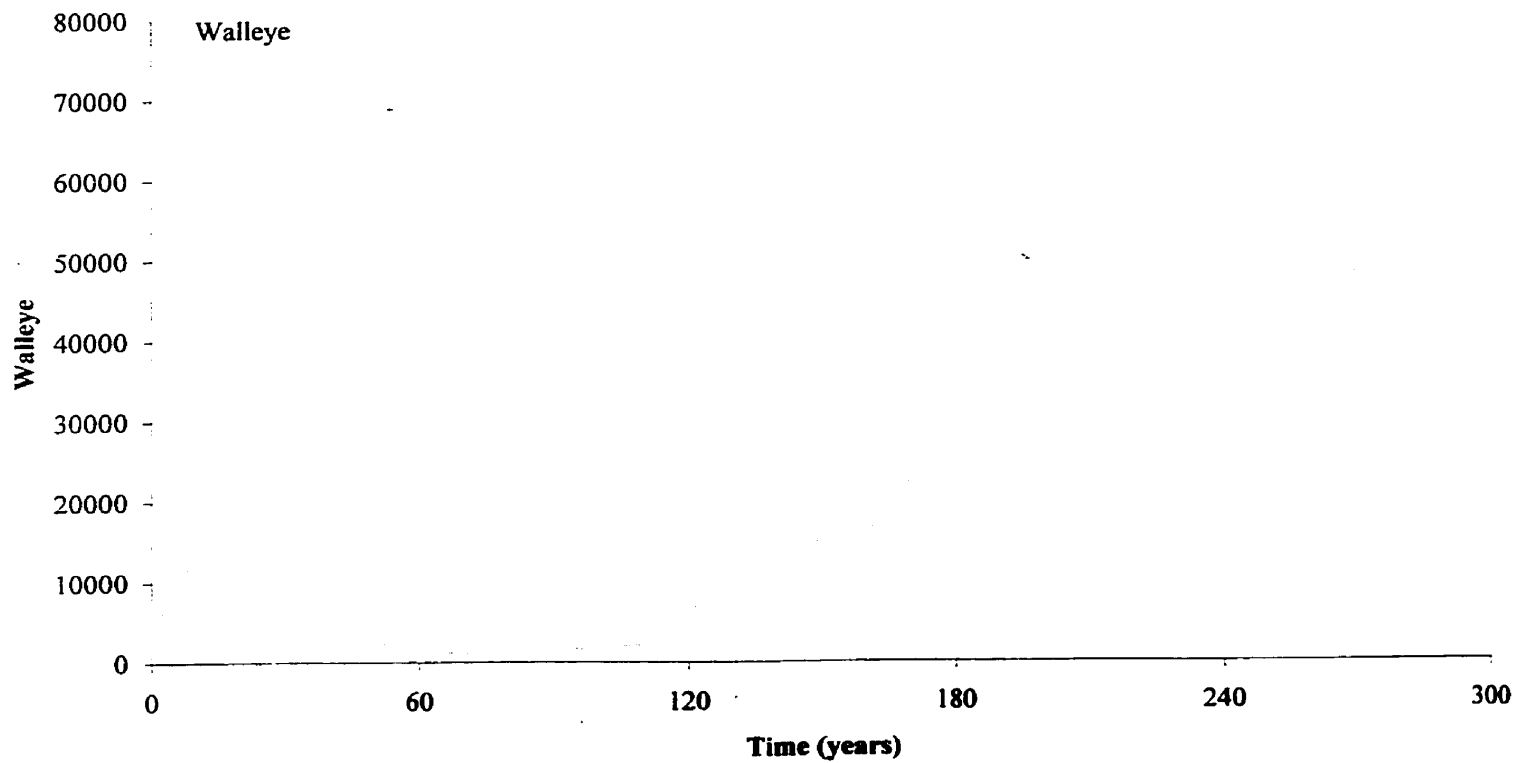
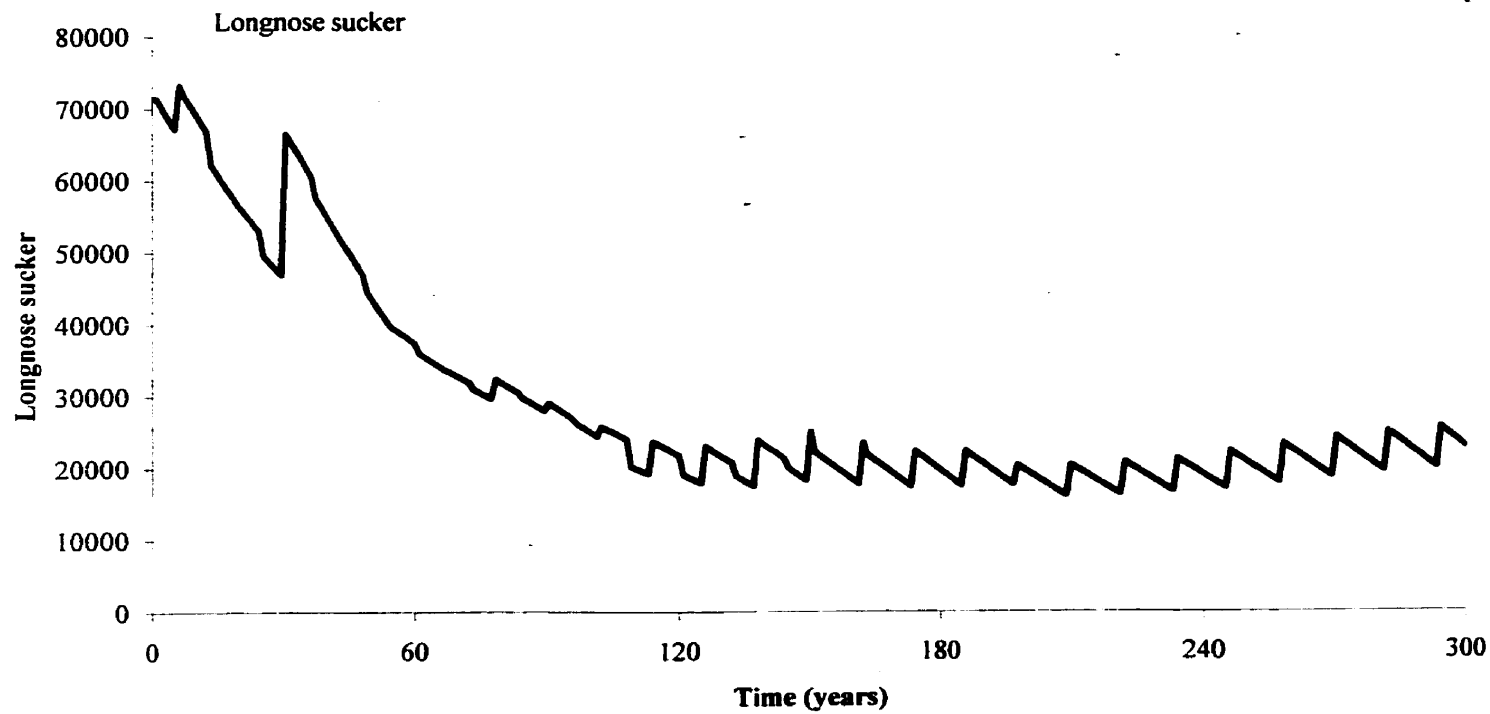


Figure 65. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario 4



Scenario 4 simulation.

abundance was approximately eight times higher relative to numbers with Scenario 1 at 38,526 (Table 5). This increasing trend can be explained by the lower water level fluctuations that occur with the winter short-term discharge strategy in comparison with historical discharge strategy. Walleye abundance increased rapidly between 10 and 15 years following impoundment. However, after 15 years, walleye numbers leveled out and remained relatively stable for the remainder of the 25 year simulation period (52,226 individuals)(Figure 65).

4.2.5 Scenario 5 - (Spring flood and Historical)

Scenarios 5 through 8 investigated the impacts of the spring flood monthly discharge strategy in combination with the four short-term strategies already discussed (refer to Table 1). It is expected that during these simulations, northern pike will benefit from the flooding of additional land area each spring. Since northern pike are considered the top predator in the reservoir ecosystem, an increase in their abundance was predicted to impact the populations of other fish species included in the model. As predicted, a dramatic increase in northern pike abundance was evident from the Scenario 5 simulation (Figure 66). Compared with Scenario 1, northern pike numbers increased over time and were approximately five times greater at 91,520 individuals, by the end of the 25 year simulation. The increase in northern pike numbers increased the amount of predation on the other fish species included in the model. As a result, longnose sucker abundance steadily decreased over time (Figure 66), and were approximately half their Scenario 1 numbers (10,835 individuals) at the end of the 25 year simulation (Table 5). Similarly, lake whitefish abundance decreased over time (Figure 66) and by the end of the 25 year simulation period, lake whitefish numbers were approximately two-thirds those of

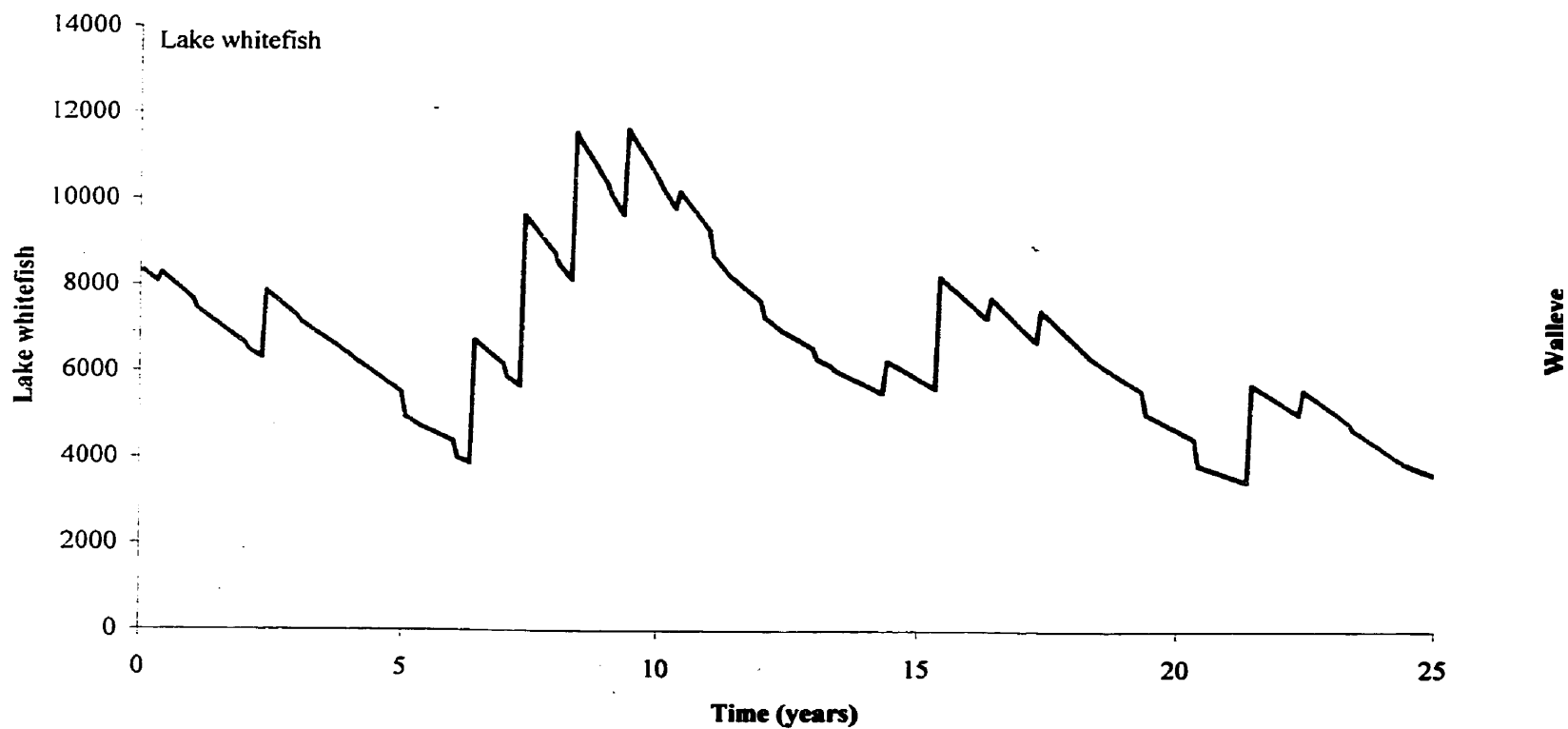
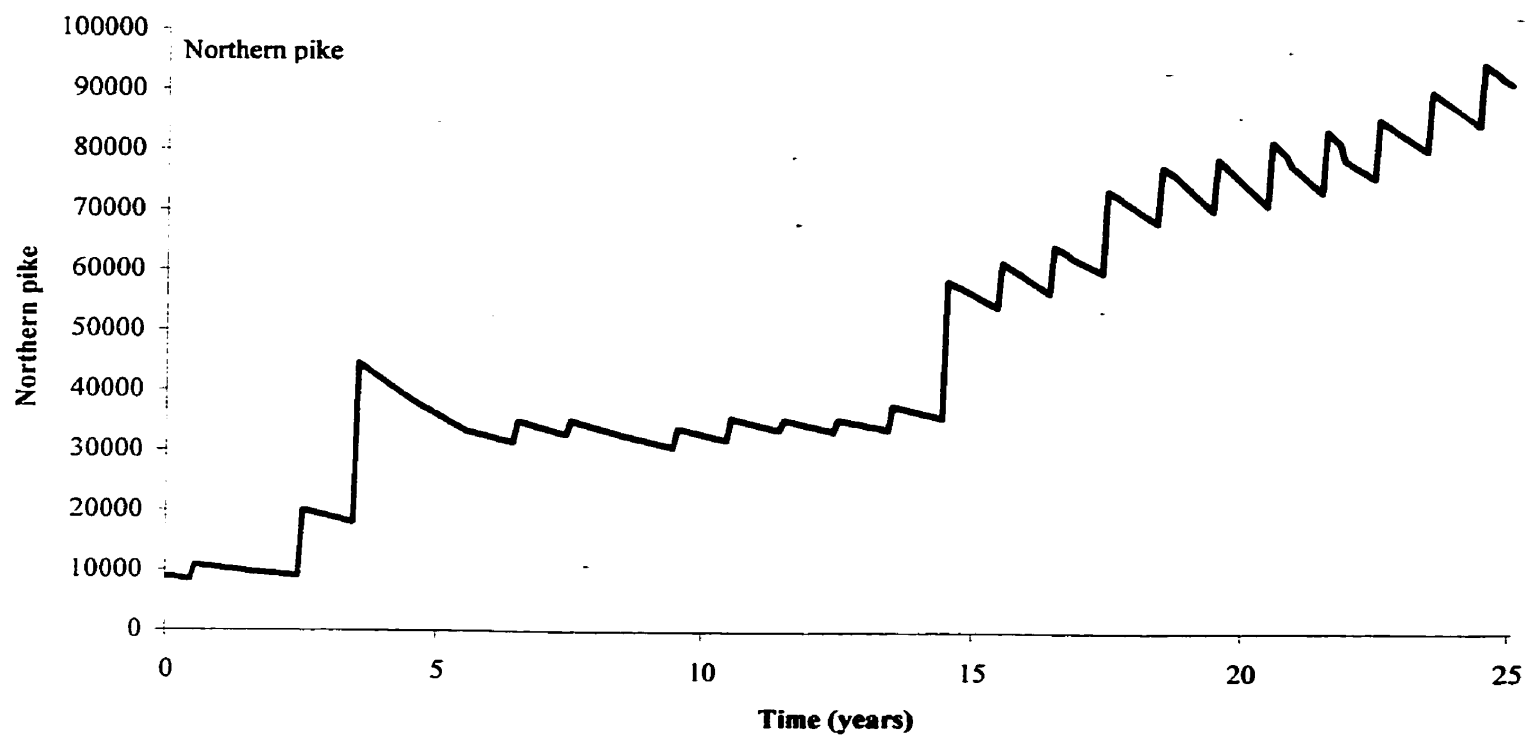
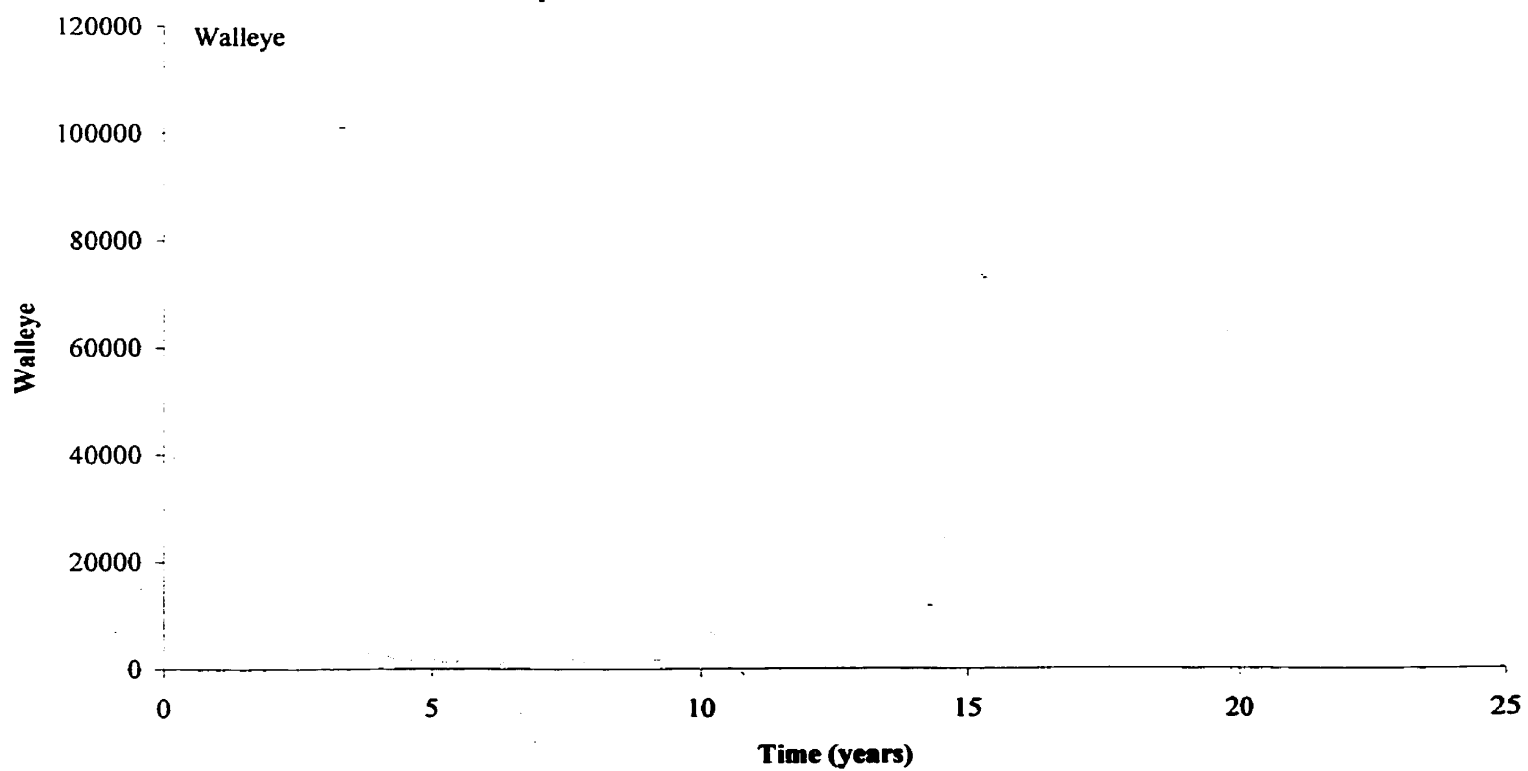
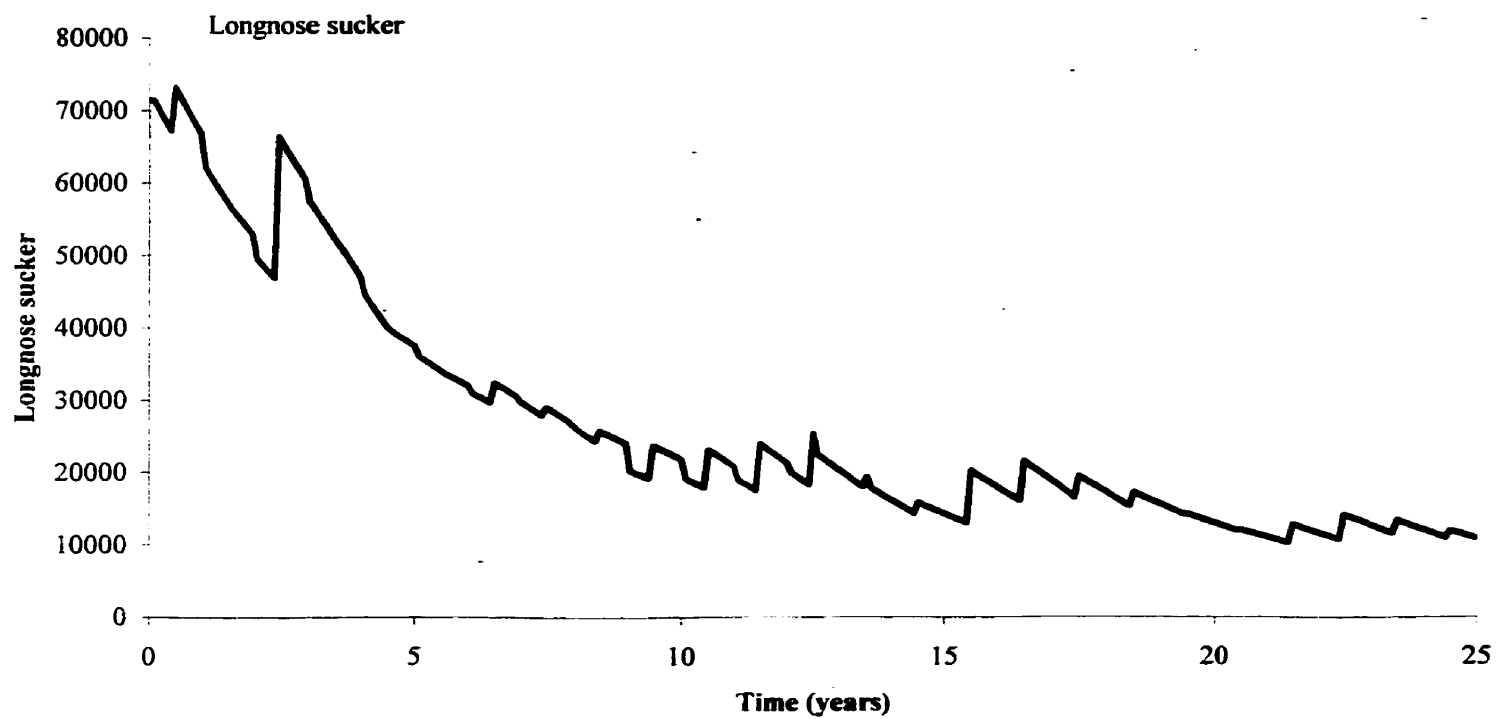


Figure 66. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario 5



the Scenario 5 simulation.

Scenario 1, at 3,656 individuals (Table 5). Walleye abundance was also negatively affected by the increase in northern pike. Although a dramatic increase in abundance was observed for their population (Figure 66), walleye numbers were found to be 66,423, approximately 10,000 individuals less than those observed with Scenario 1 (Table 5).

4.2.6 Scenario 6 - (Spring flood and extreme)

The results of Scenario 6 suggested that all fish species were negatively impacted by the extreme short-term discharge strategy which caused water level fluctuations of over 2 m in each reservoir region (Figure 67). The results were similar to Scenario 2 where all fish populations decreased significantly in the reservoir over time. Populations of lake whitefish and walleye were reduced to zero, while northern pike and longnose sucker numbers would also reach zero if the simulation were allowed to proceed for longer time period (Table 5). Results indicated that high water level fluctuations (caused by the extreme discharge strategy) could limit populations of fish in a hydroelectric reservoir.

4.2.7 Scenario 7 – (Spring flood and stable)

The discharge strategies tested with Scenario 7 were considered optimal for the northern pike population. Additional flooded area each spring, combined with stable water levels, contributed to the highest number (99,342) of northern pike that occurred with any Scenario analyzed in this study (Figure 68) (Table 5). Longnose sucker abundance decreased for a 10 year period following reservoir development. Subsequently, the abundance of longnose sucker increased and leveled off 15 years after impoundment (Figure 68). Longnose sucker numbers were higher than Scenario 1 at 31,472, but lower than Scenario 3, due to the increased number of northern pike relative to Scenario 3. The abundance of lake whitefish increased significantly with the Scenario

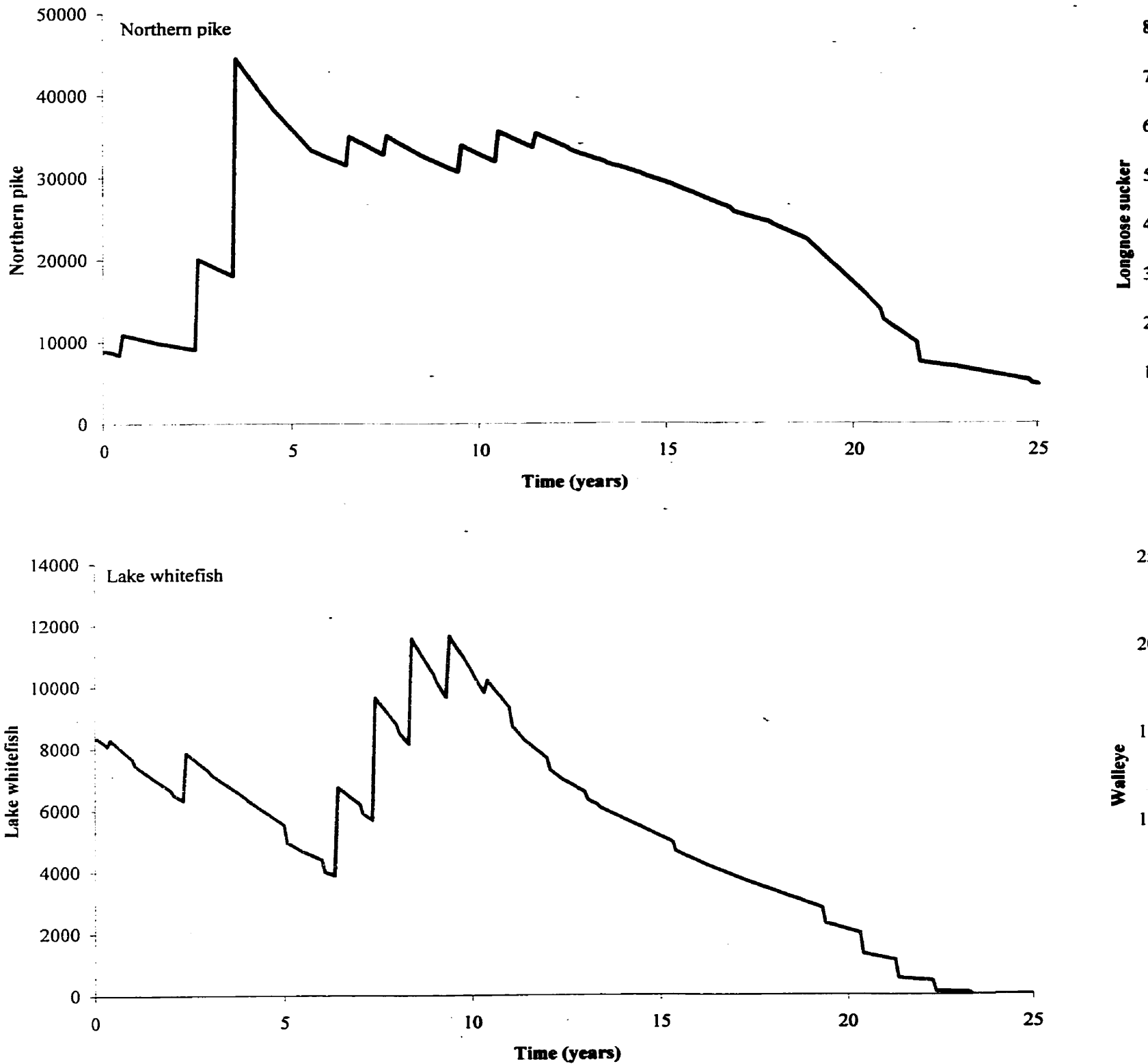
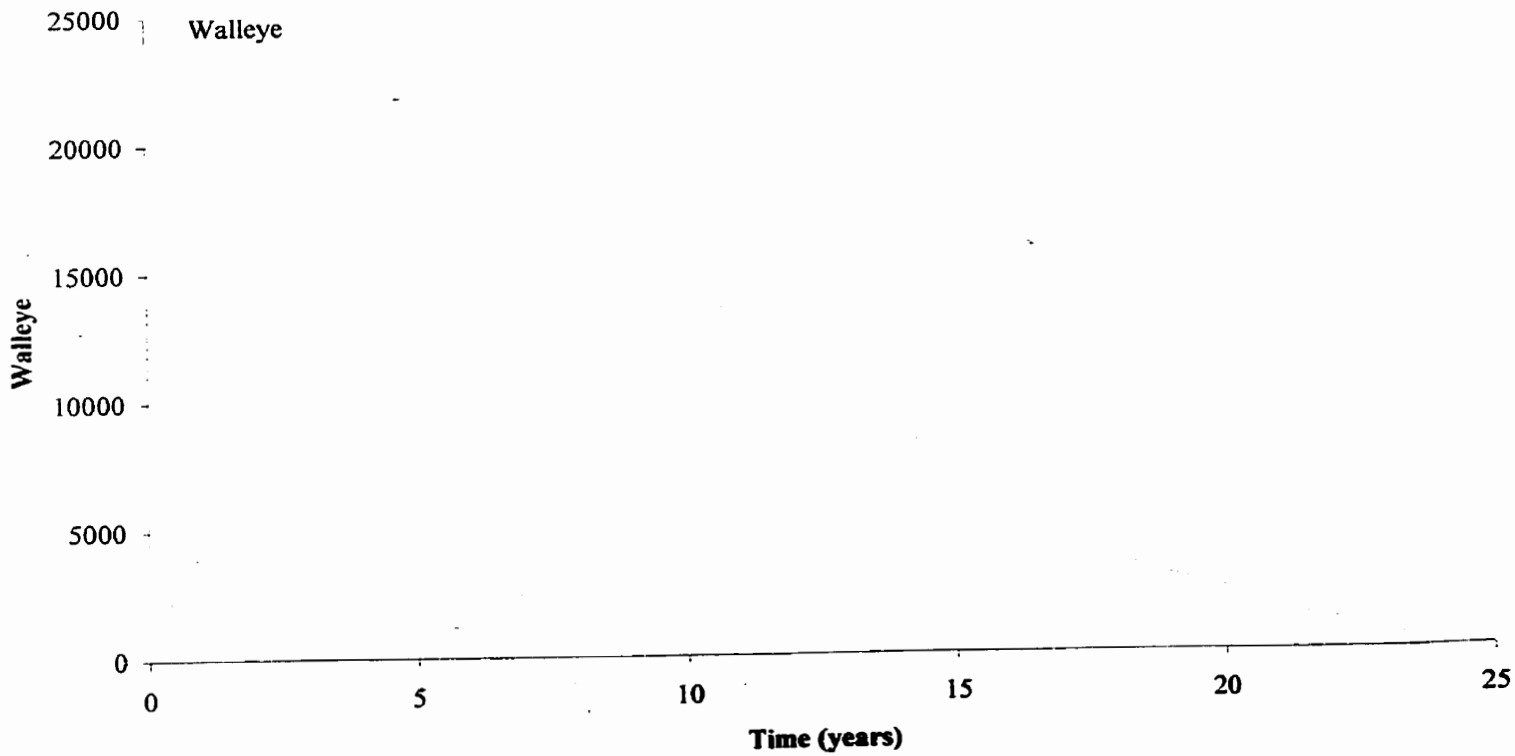
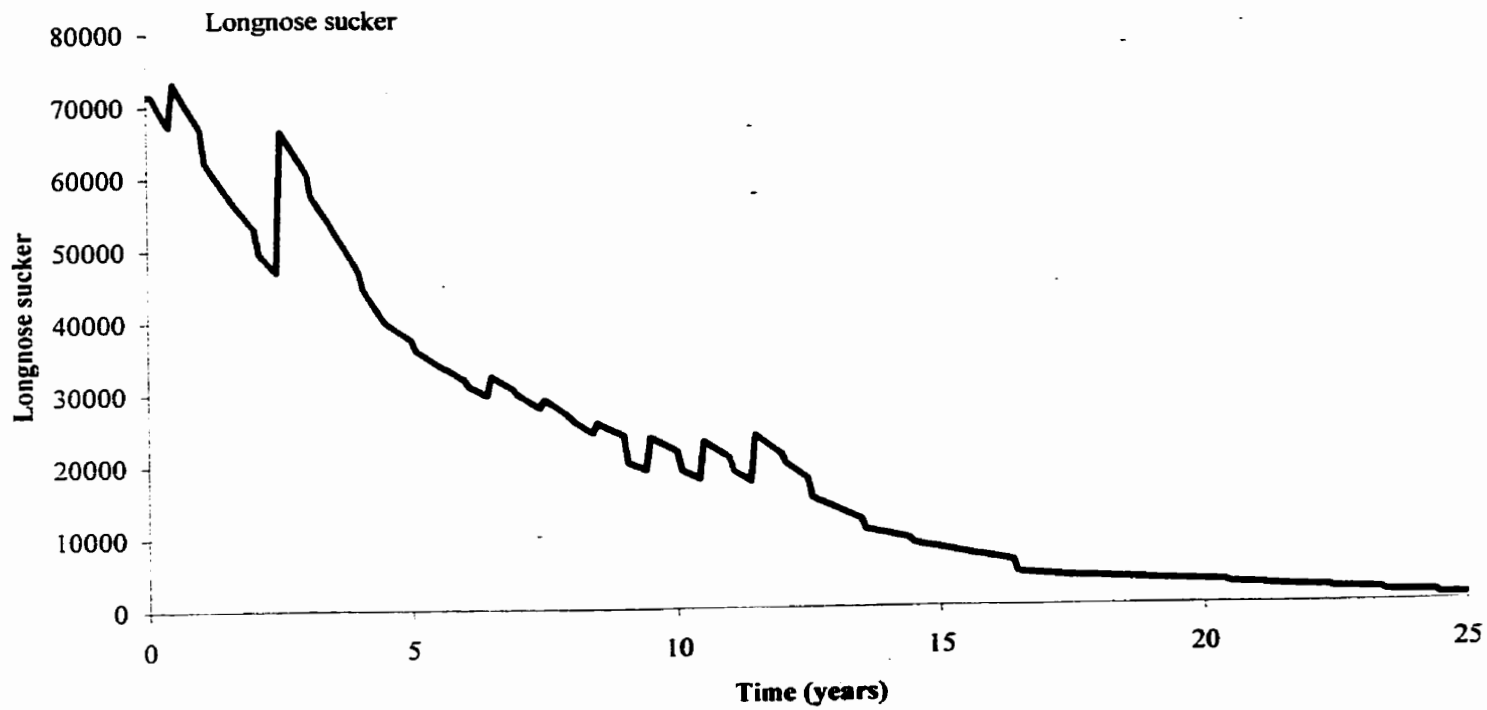


Figure 67. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario 6 si



Scenario 6 simulation.

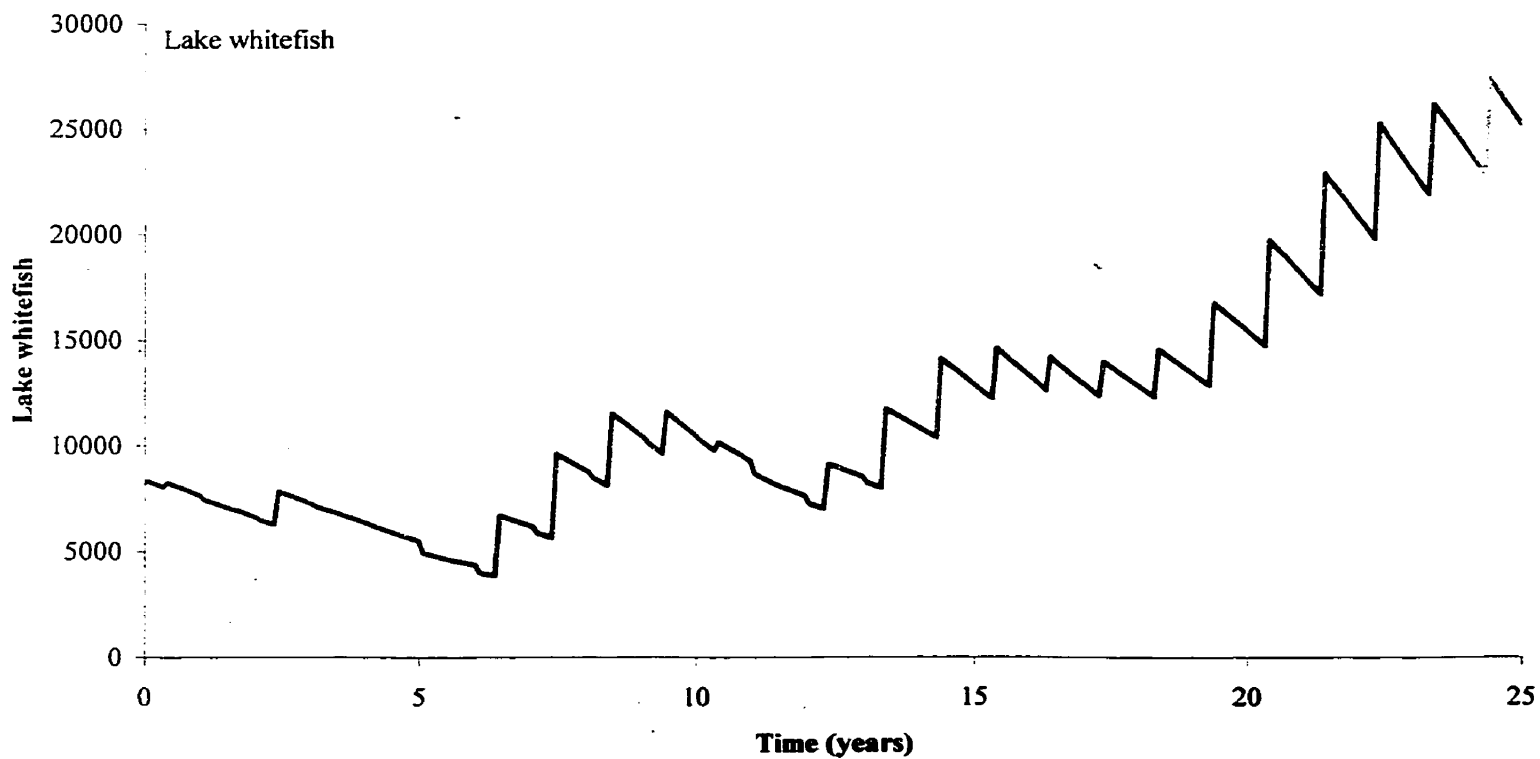
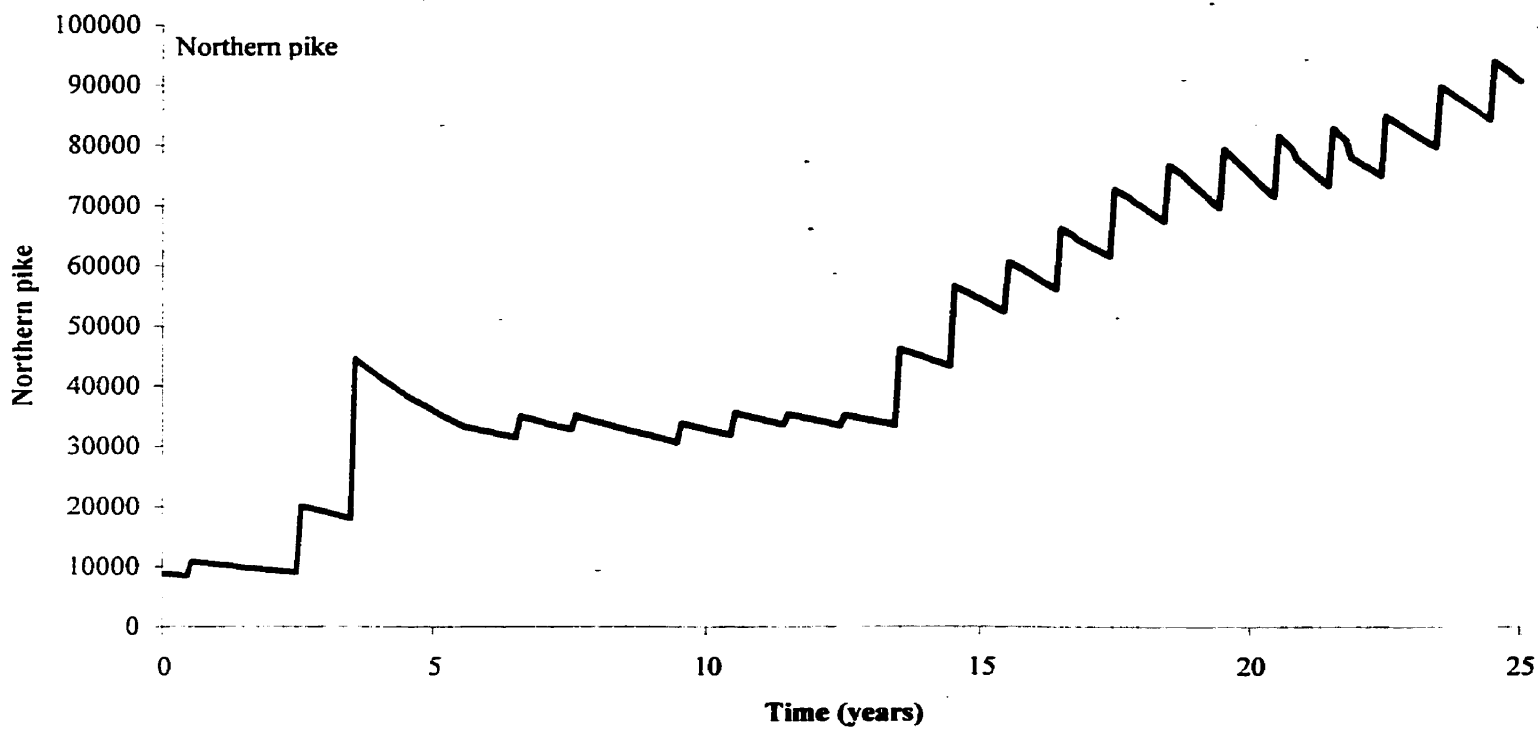
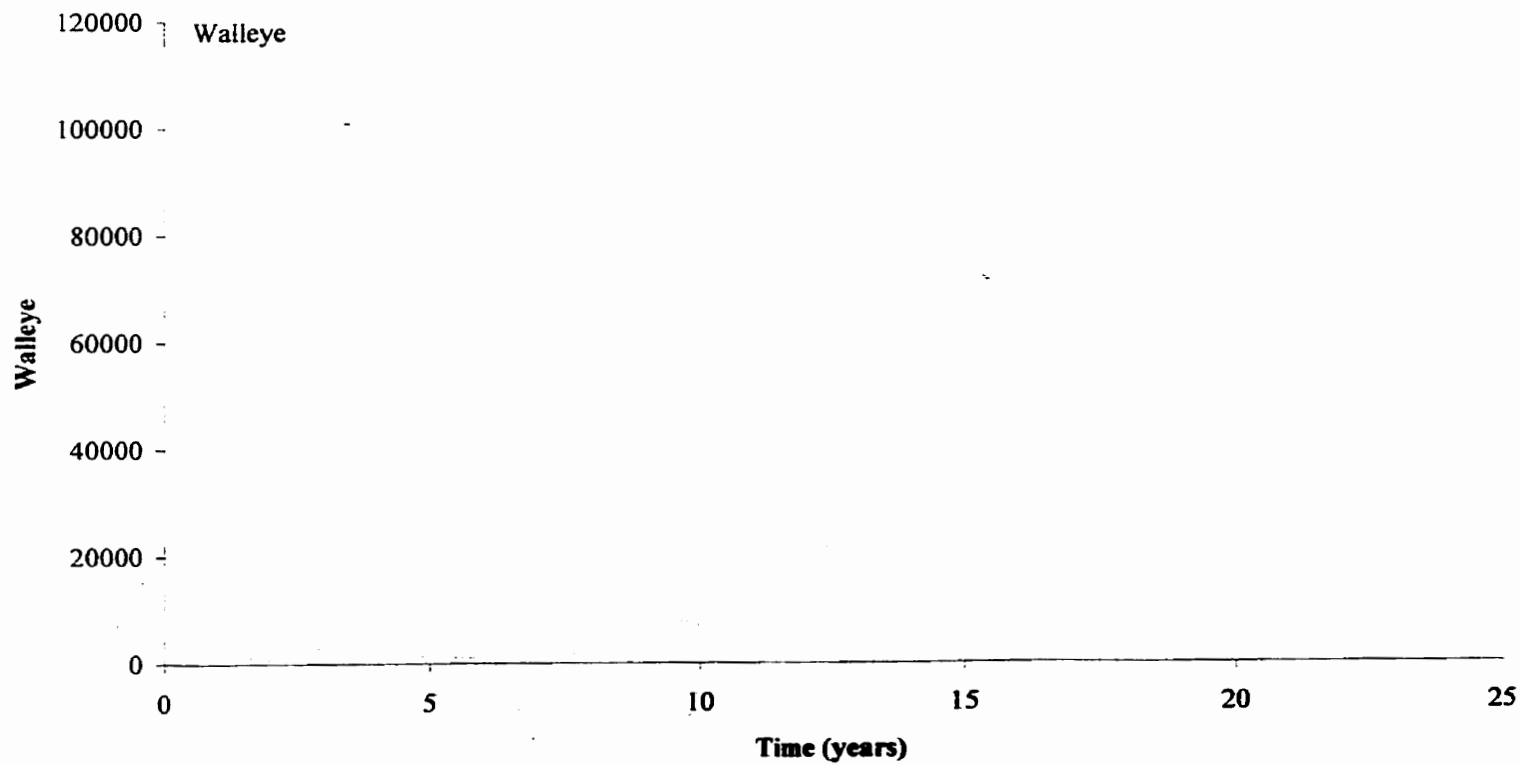
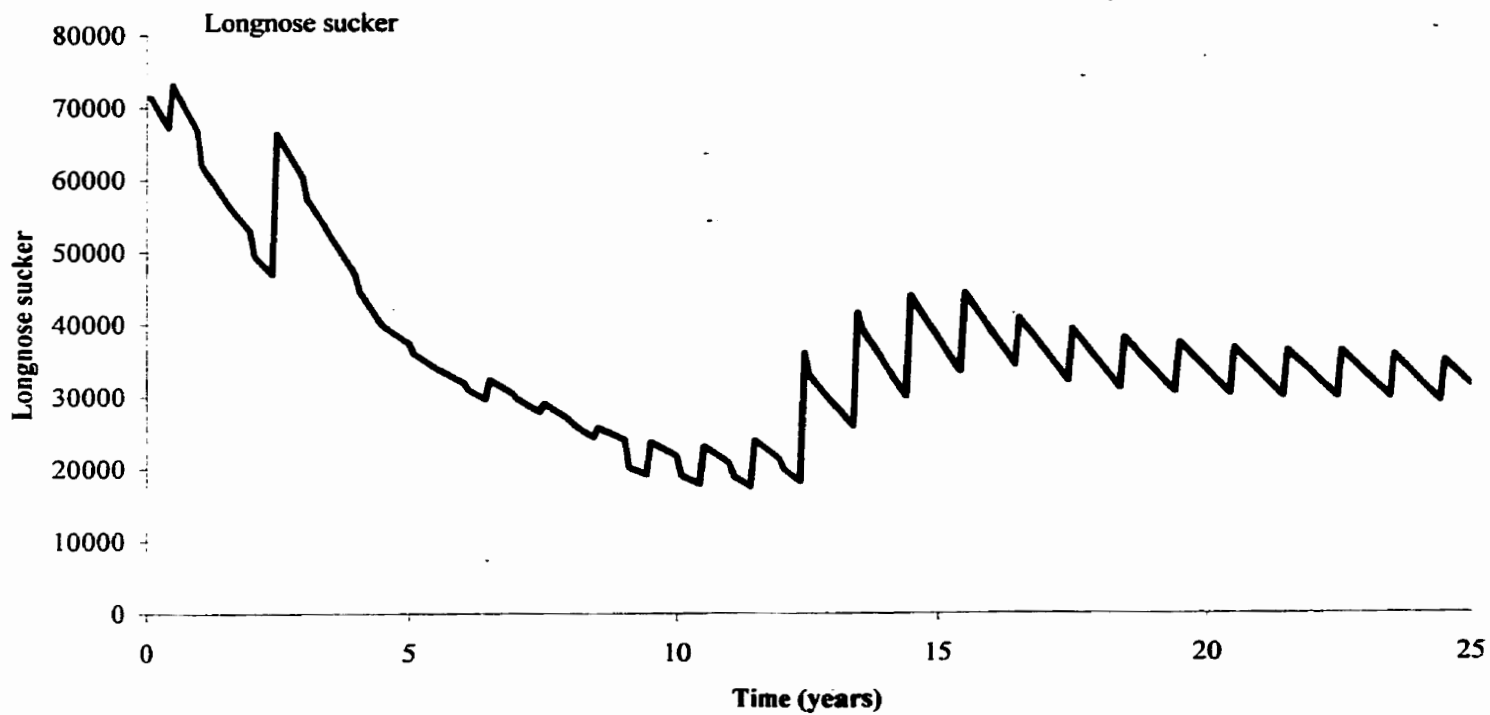


Figure 68. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario 7



the Scenario 7 simulation.

7 simulation (Figure 68). In comparison to Scenario 1, lake whitefish numbers were approximately 11 times greater, at 72,947 (Table 5). This suggested that stable water levels may be a more important influence on lake whitefish numbers than predation from northern pike. Walleye abundance increased in the reservoir with the Scenario 7 simulation, however, their numbers were found to be lower than Scenario 1 at 63,216 (Table 5). Similar to the Scenario 3 simulation, this result may be due to a more rapid growth of their population which increased the amount of cannibalism (Figure 68).

4.2.8 Scenario 8 – (Spring flood and Winter)

As with the other operating strategies investigated with the spring flood seasonal operating strategy, northern pike abundance increased significantly to approximately four times (90,849) their numbers with Scenario 1 (Table 5) (Figure 69). Longnose sucker abundance decreased steadily over time in the reservoir (Figure 69) and their population was two times lower than Scenario 1, at 10,258 individuals, by the end of the simulation (Table 5). The increase in northern pike numbers relative to Scenario 1 was the main factor which contributed to this decreasing trend. Lake whitefish abundance increased over time (Figure 69), however, the increase was not as significant as the increase observed in Scenario 4, due to the higher number of northern pike relative to Scenario 4. Numbers of lake whitefish were 25,320, five times their Scenario 1 abundance, by the end of the 25 year simulation period (Table 5). Walleye numbers were lower relative to Scenario 1 and reached 47,816 at the end of the simulation. Although an increasing trend was observed in the reservoir over time with Scenario 8 (Figure 69), pike predation and cannibalism contributed to these lower numbers.

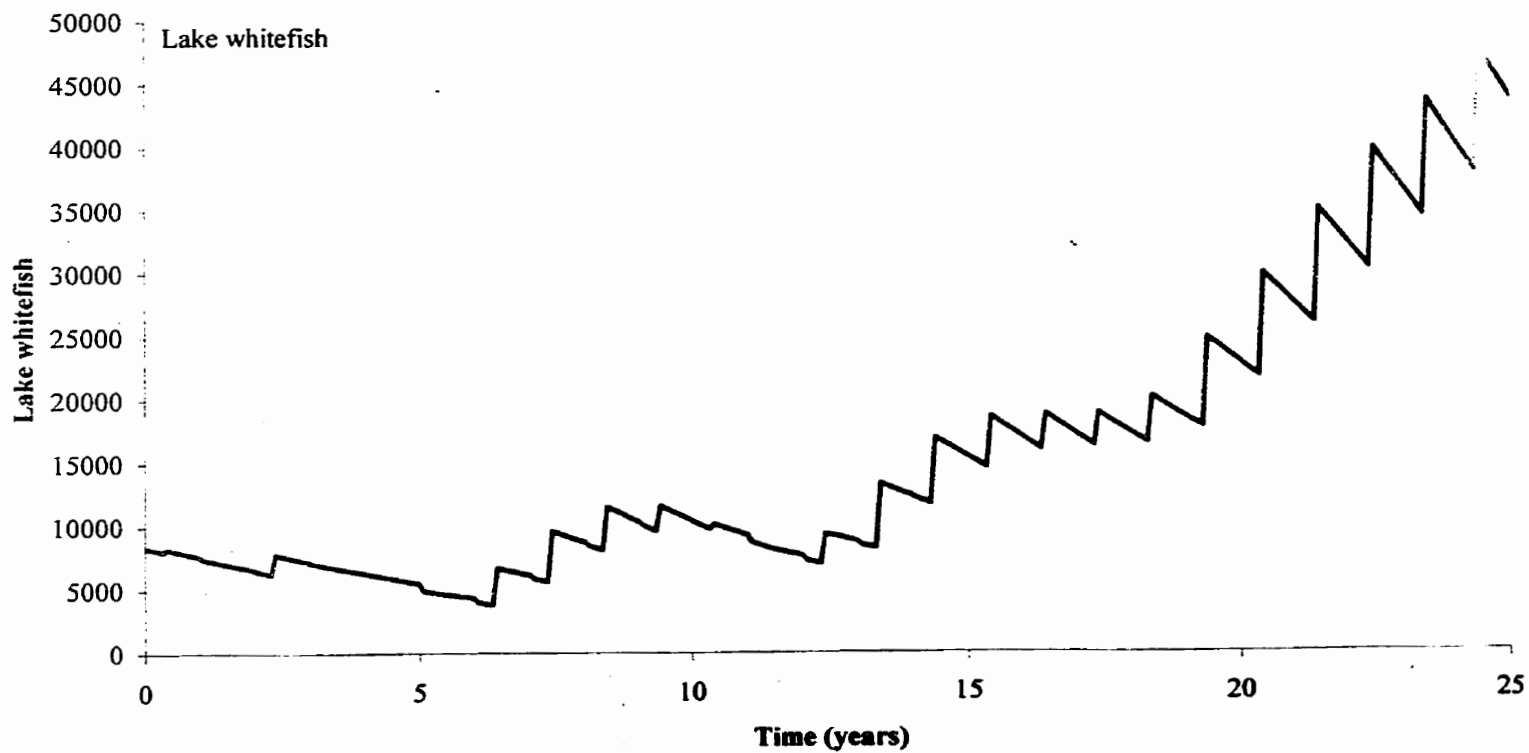
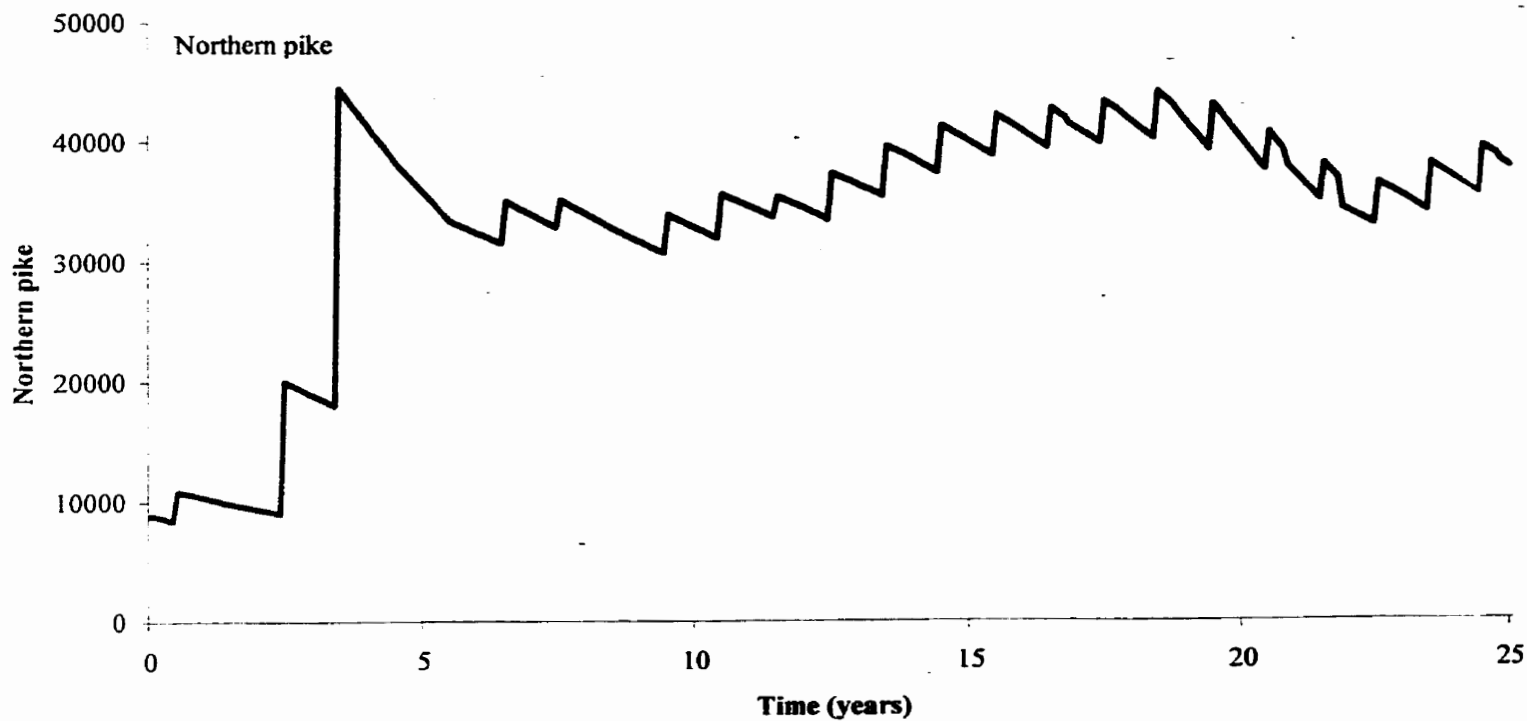
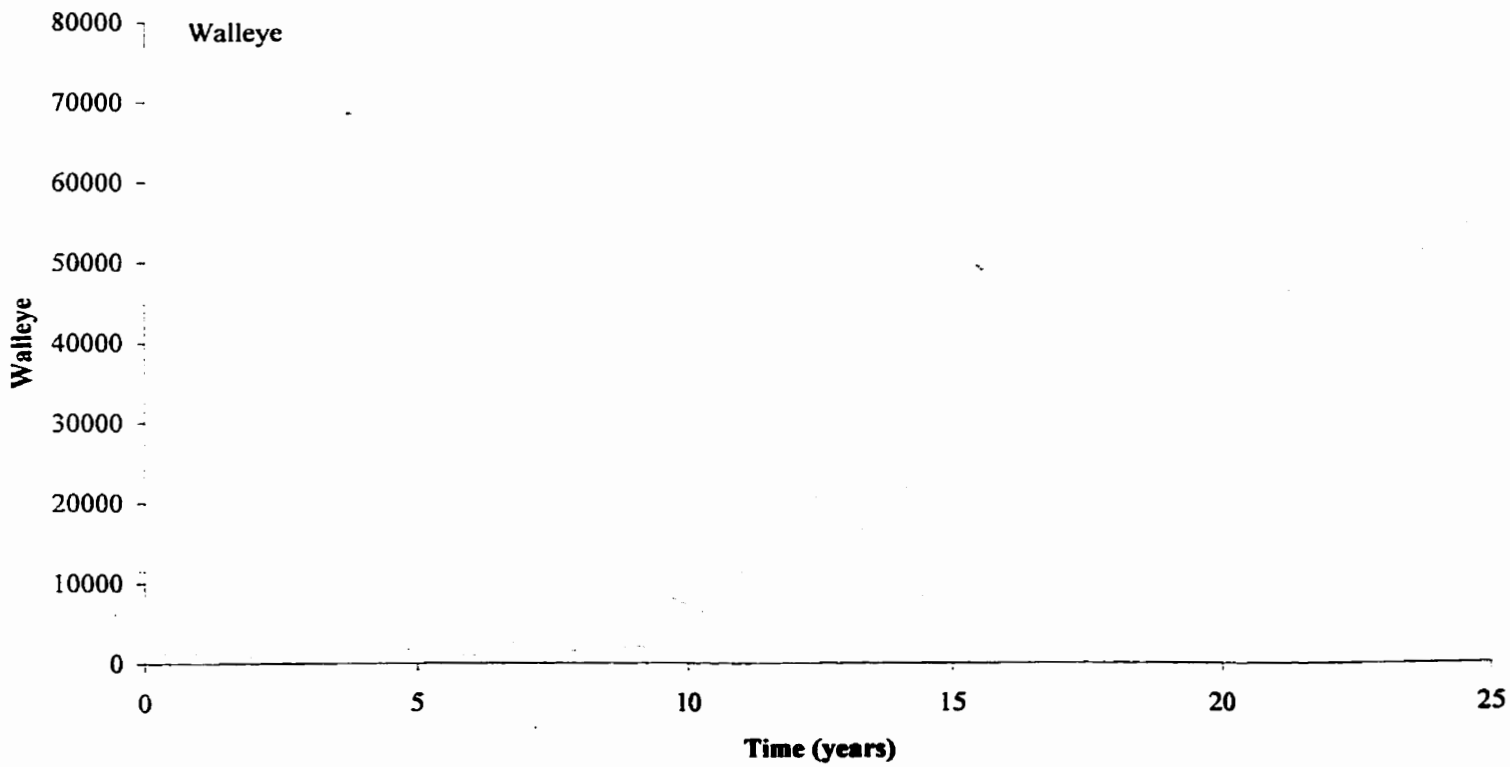
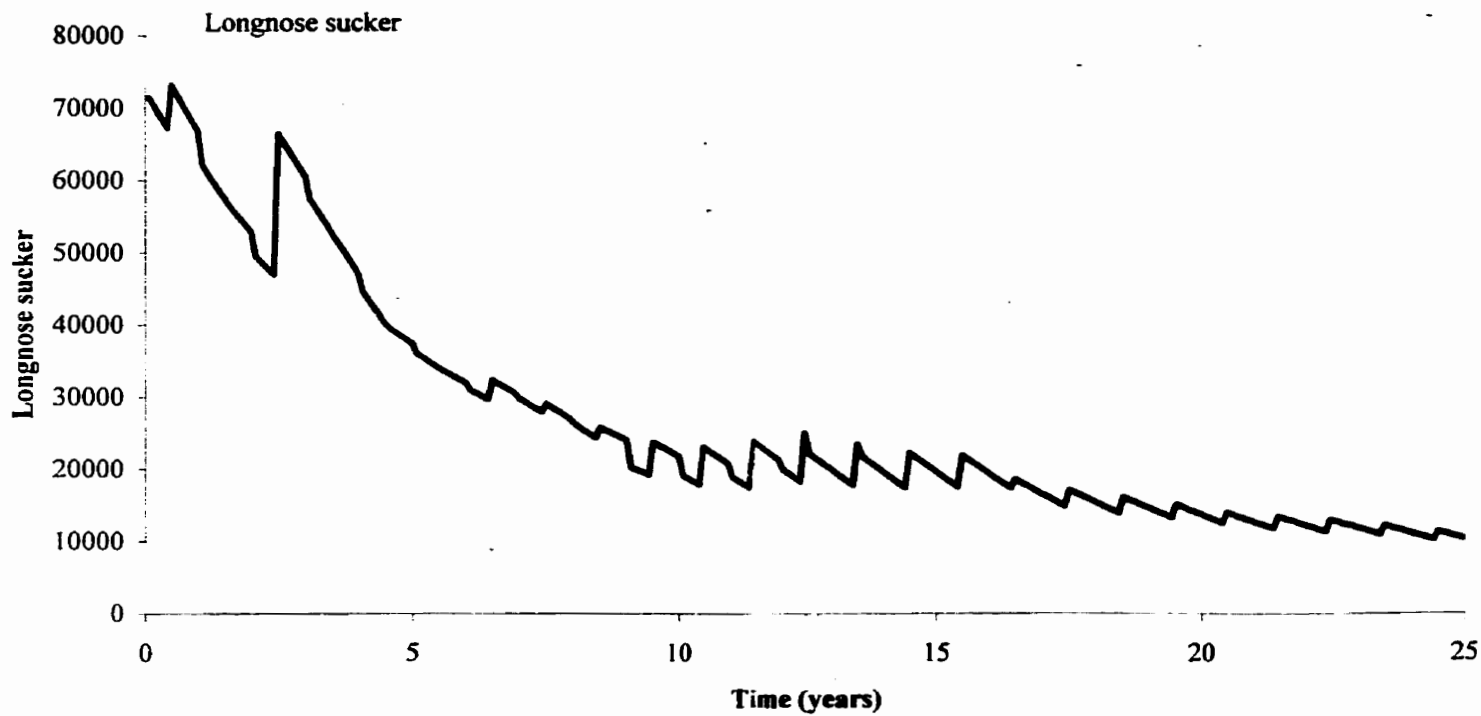


Figure 69. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Scenario



the Scenario 8 simulation.

4.3 FISH – Alternating strategies

The above eight scenarios used historical data for the first 10 years of the model simulation. After this 10 year period, the same monthly discharge strategy, and the same short-term discharge strategy, was used each month for the remaining 15 years of the simulation. The following alternative strategies investigate the impact of changing the short-term strategy during the year. For example, Alternative 1 used the stable short-term operating strategy in April, May and June, the historical short-term strategy in July and August and the winter short-term operating strategy for the remainder of the year (refer to Table 2). The purpose of this exercise was to investigate how alternating short-term operating strategies over the course of a year would impact fish abundance in the reservoir. Also, these simulations may identify periods of the year in which certain fish species are more susceptible/vulnerable to short-term hydro operations strategies.

4.3.1 Alternative 1

This alternative strategy employed the stable operating strategy during April, May and June, the historical operating strategy during July and August, and the winter operating strategy for the remainder of the year (Table 1).

In general, maintaining stable water levels during spring benefited the spawning success of northern pike, longnose sucker and walleye, since these fish species spawn during the spring. Northern pike abundance increased four years after impoundment and remained relatively stable for the remainder of the simulation (Figure 70). Northern pike numbers doubled relative to Scenario 1 to 39,184 individuals (Table 5). Longnose sucker abundance decreased for the first 15 years after impoundment and subsequently leveled off (Figure 70). At the end of the simulation their numbers were approximately 75% of

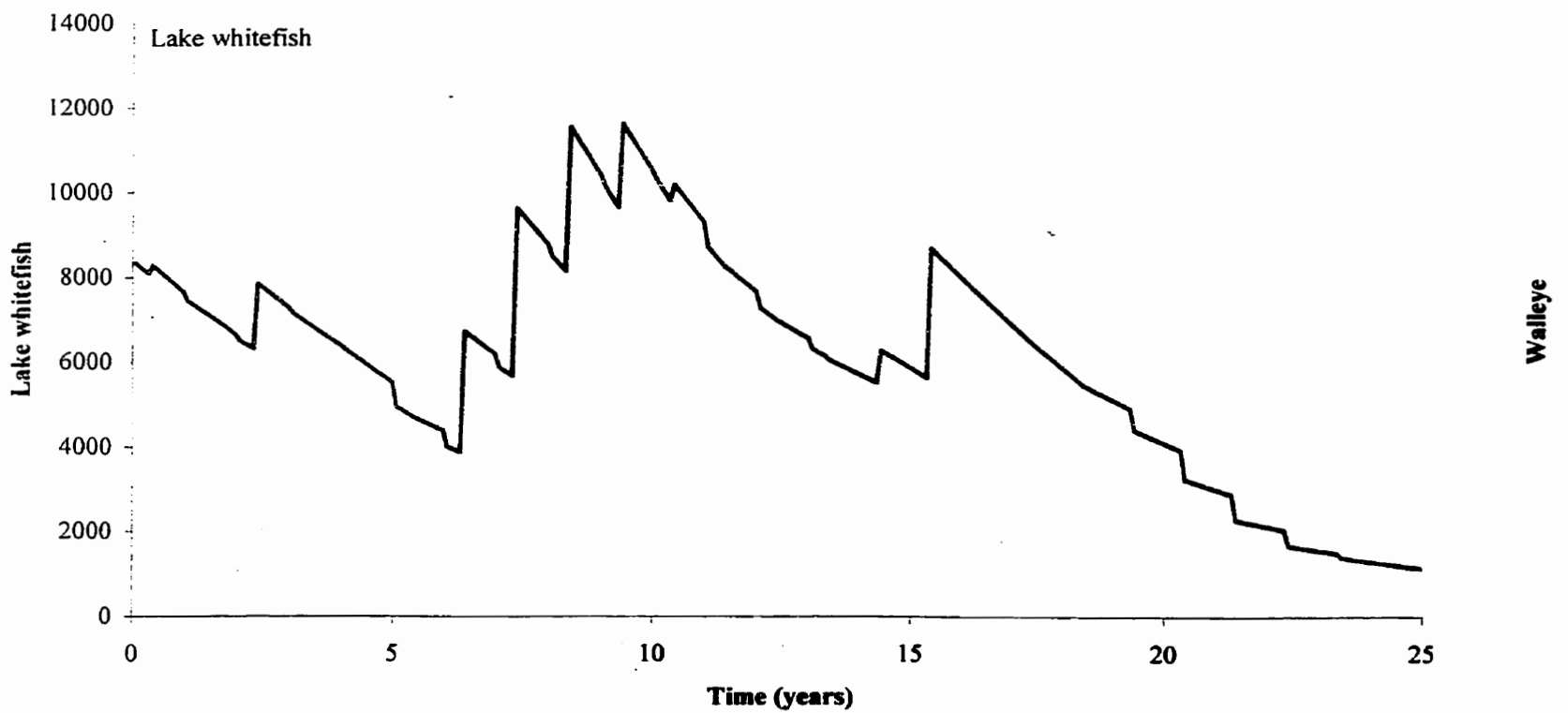
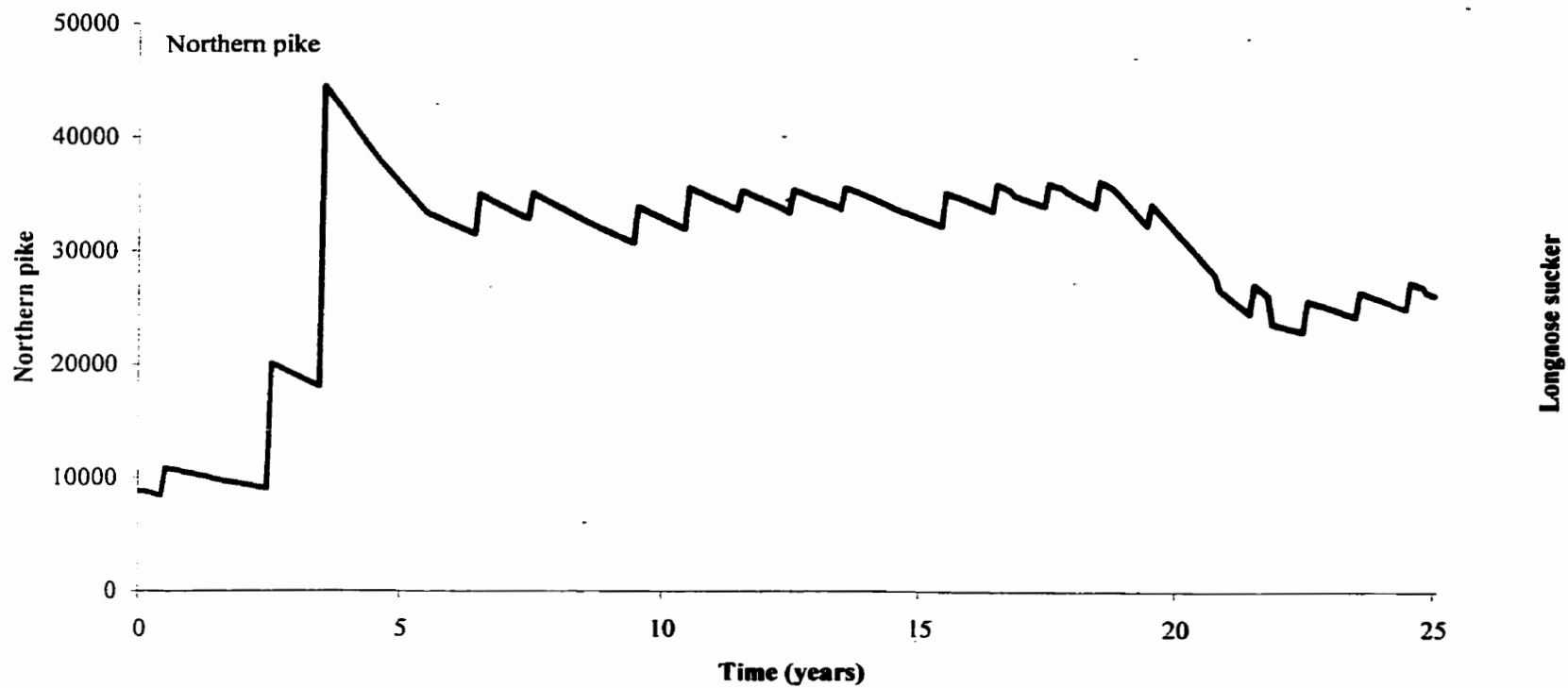
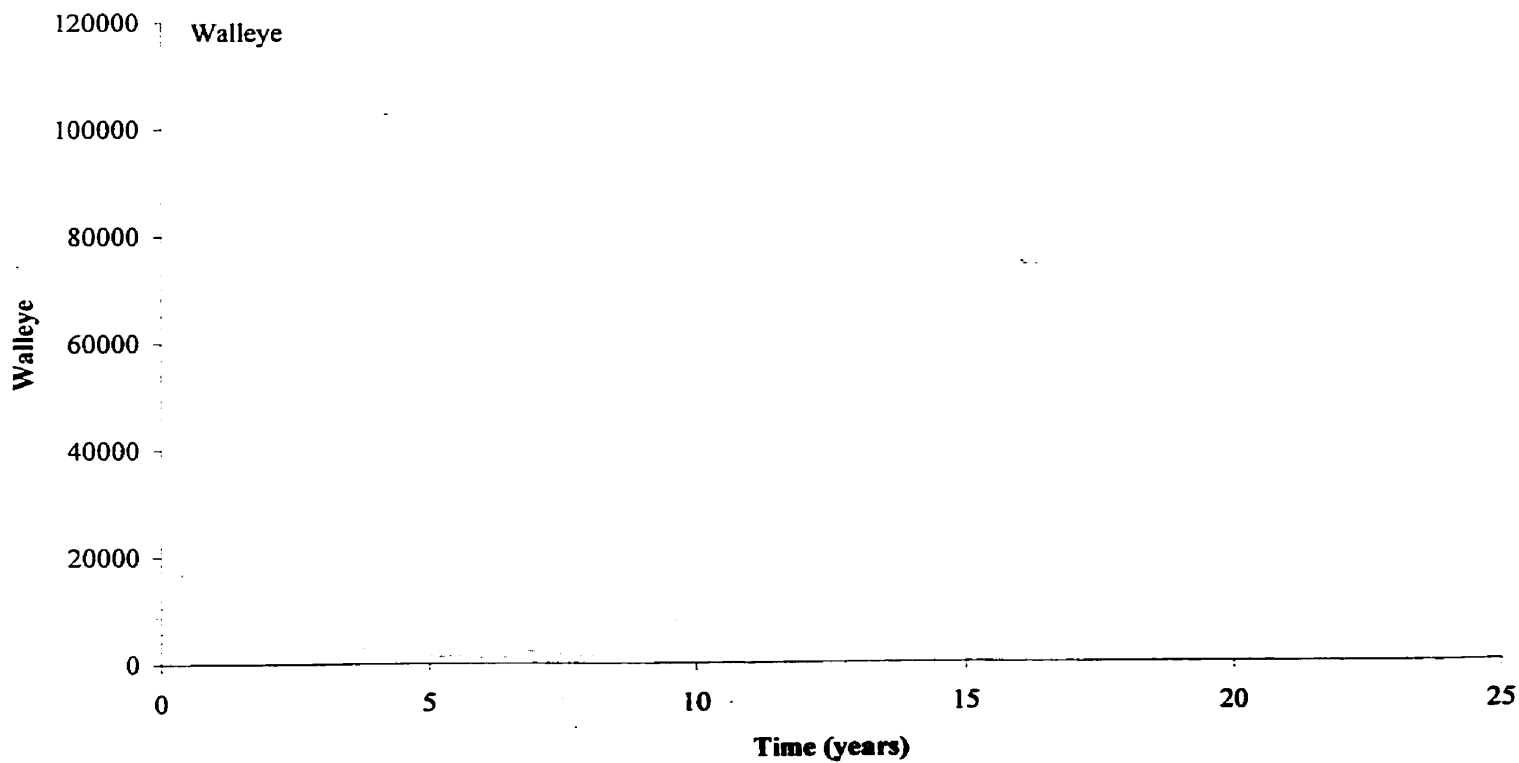
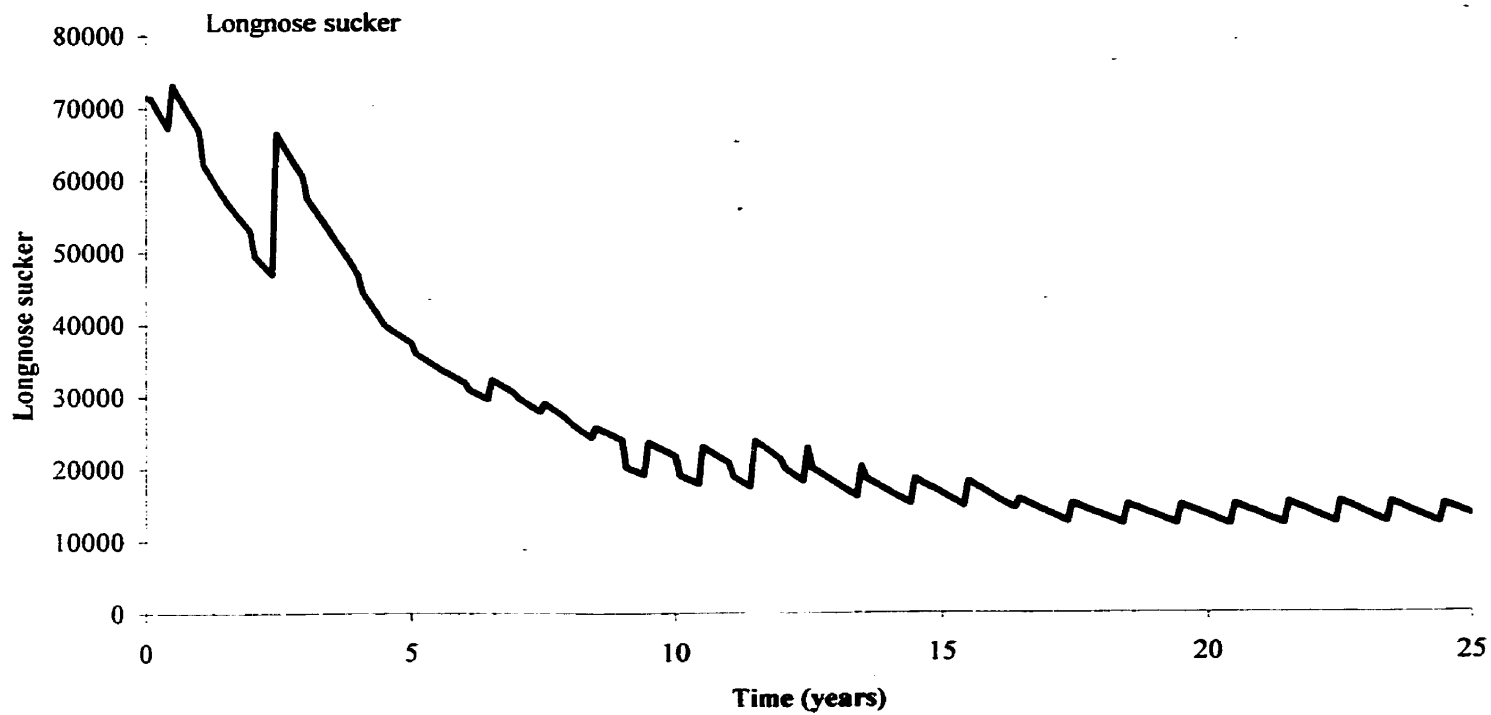


Figure 70. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Alternative 1



Alternative 1 simulation.

their numbers observed with Scenario 1, at 14,959 (Table 5). This decrease was due to increased predation from northern pike and walleye. Lake whitefish abundance increased significantly over the course of the 25 year simulation to 42,474 individuals, approximately eight times their Scenario 1 numbers (Table 5) (Figure 70). This increase was due to the winter operating strategy which results in smaller water level fluctuations during the lake whitefish egg incubation period. Walleye abundance increased significantly in the reservoir with the Alternative 1 simulation (Figure 70). Results indicated that their numbers were slightly lower than Scenario 1 at 69,340 individuals at the end of the simulation. However, this result was due to a more rapid increase in the walleye population which subsequently increased cannibalism, and reduced their numbers (Table 5).

4.3.2 Alternative 2

The Alternative 2 combination of short-term discharge strategies involved employing the historical short-term operating strategy during April, May, June, July, August, and September, and the stable operating strategy during October, November, December, January, February, and March.

With the Alternative 2 simulation, populations of spring spawning fish species were affected in a similar way as Scenario 1 since the historical discharge strategy was employed during spring. The northern pike population increased four years after impoundment due to the increase in flooded area, and subsequently decreased in number to 23,527 individuals by the end of the 25 year simulation period (Table 5) (Figure 71). Similarly, trends observed in longnose sucker and walleye abundance were comparable to Scenario 1, their numbers were 22,716 and 52,226, respectively. However, lake

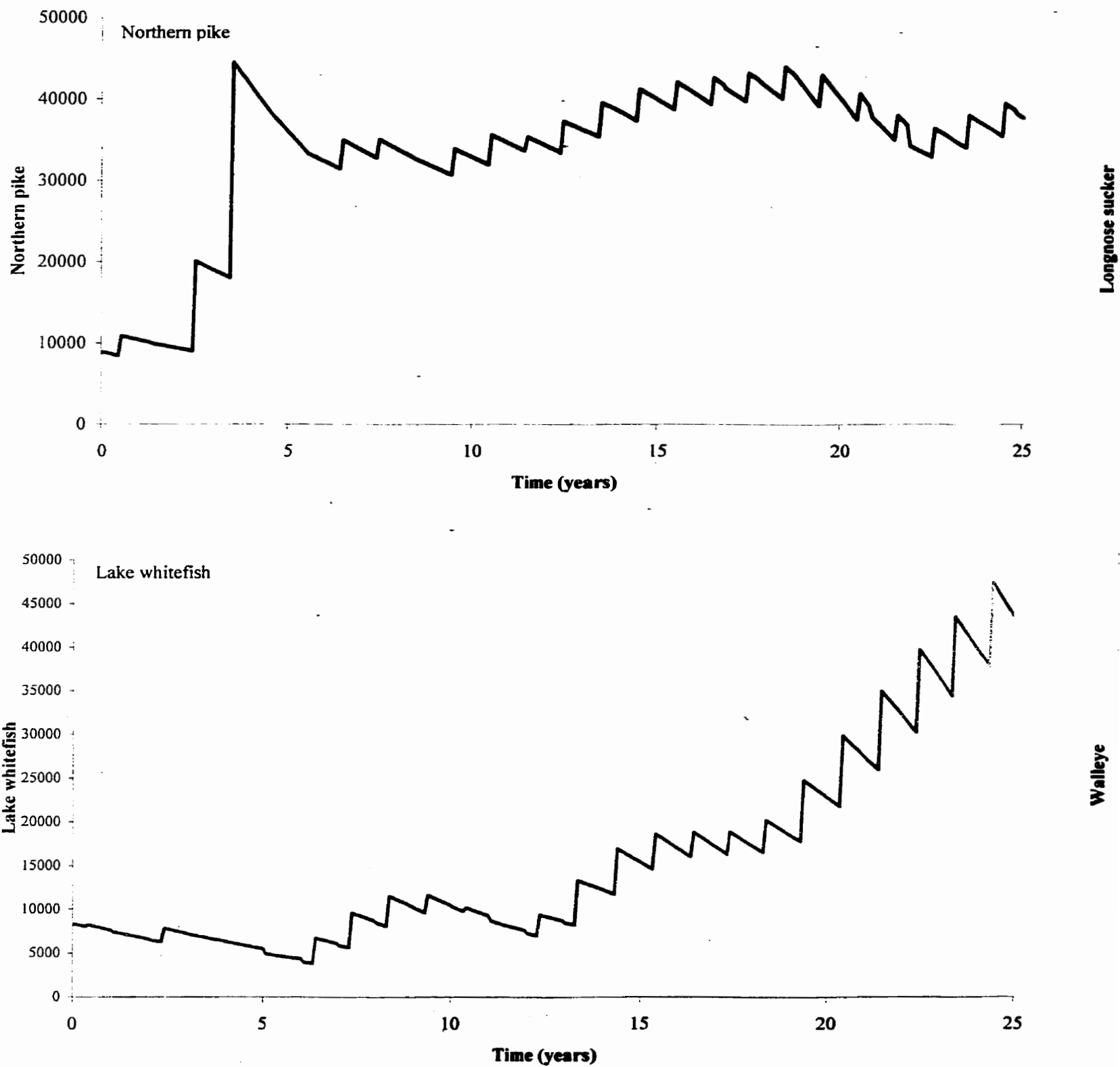
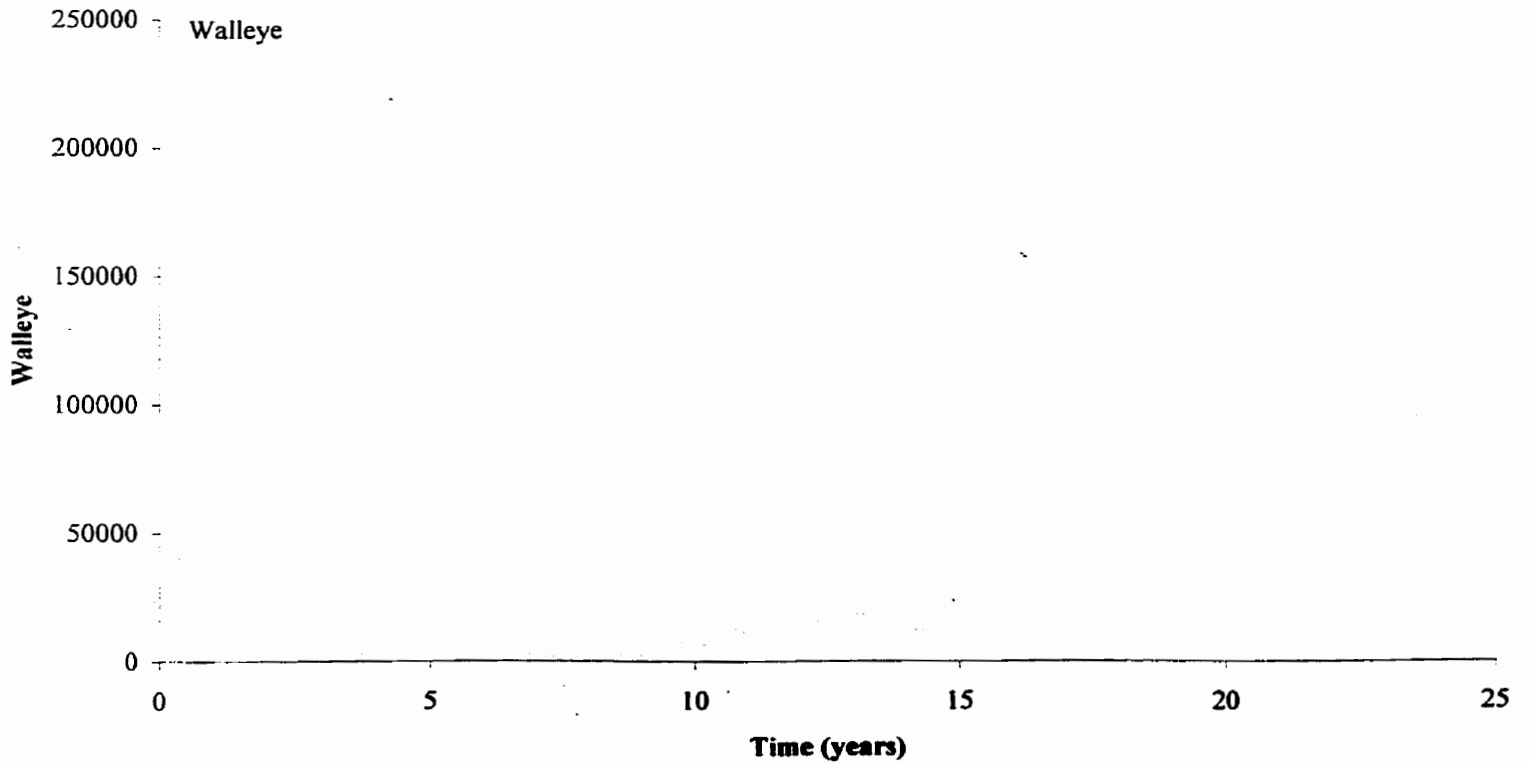
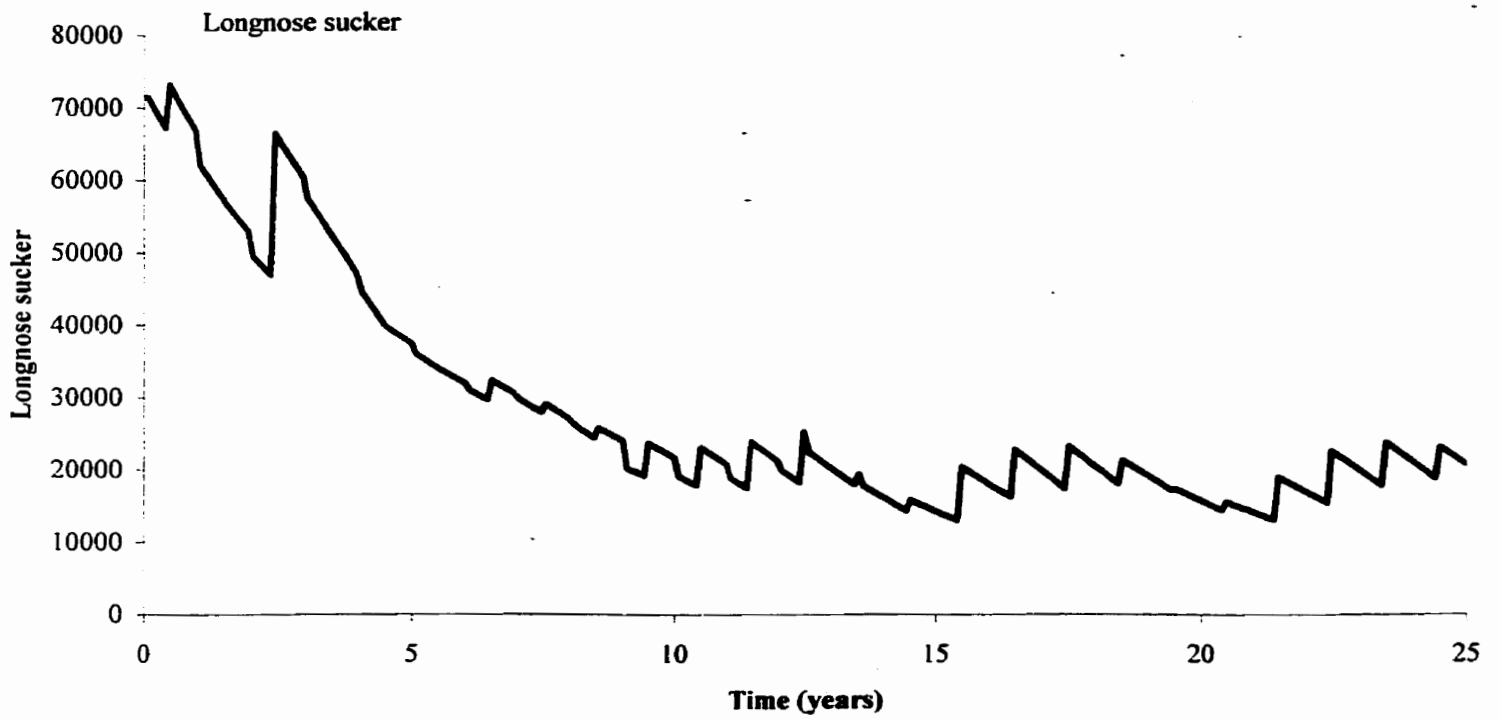


Figure 71. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Alternative



Alternative 2 simulation.

whitefish abundance increased significantly with the Alternative 2 simulation. Their numbers reached 104,022 at the end of the 25 year simulation period (Table 5), the highest lake whitefish numbers of all the discharge strategies analyzed in this thesis. In comparison with Scenario 1, their abundance was approximately 20 times greater. This can be explained by stable water levels during winter (which increased lake whitefish spawning success), moderate water levels fluctuations during spring (which does not allow for large increases in the predatory fish species), and a lack of flooded area during spring, (which does not allow for a large increase in the northern pike population).

4.3.3 Alternative 3

The third alternative employed the stable operating strategy during May, the historical operating strategy during June, the extreme operating strategy during July, August and September, and the winter operating strategy for the remaining months.

Northern pike abundance approximately doubled relative to Scenario 1 to 37,728 individuals (Table 5). Their population increased following impoundment and remained relatively stable until the end of the 25 year simulation (Figure 72). Longnose sucker decreased relative to Scenario 1 to 13,402 (Table 5). This was attributed mainly to the increased number of northern pike relative to Scenario 1 (Figure 72). Lake whitefish abundance increased significantly and was eight times greater than their Scenario 1 numbers, at 43,722. This results of Alternative 3 for lake whitefish were similar to Scenario 4 when the winter operating strategy was used during the winter months (Table 5) (Figure 72). Walleye numbers reached 69,480 by the end of the 25 year simulation period and exhibited a trend similar to Scenario 1. During the Alternative 3 simulation, walleye numbers increased rapidly between 10 and 15 years after impoundment and

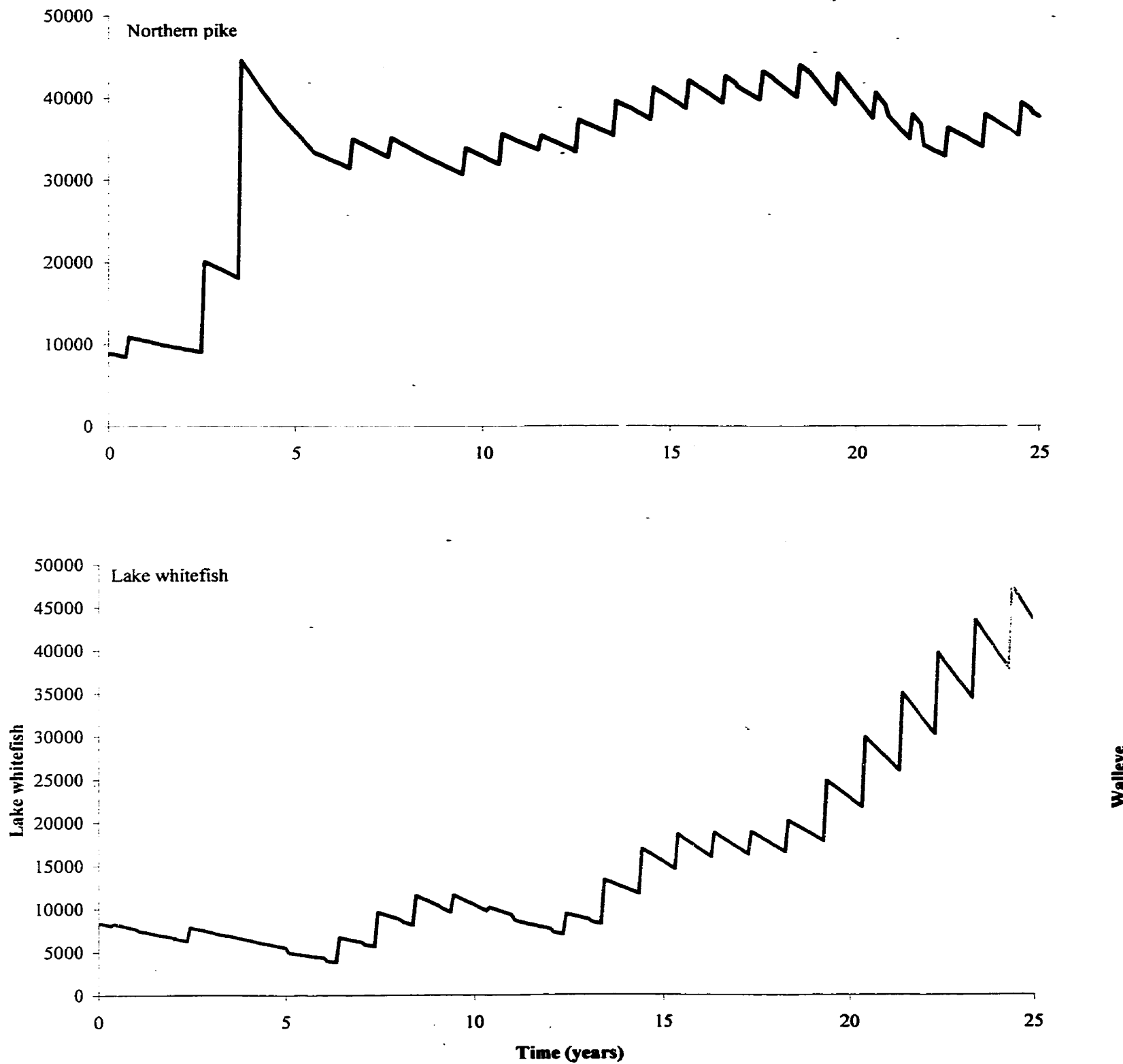
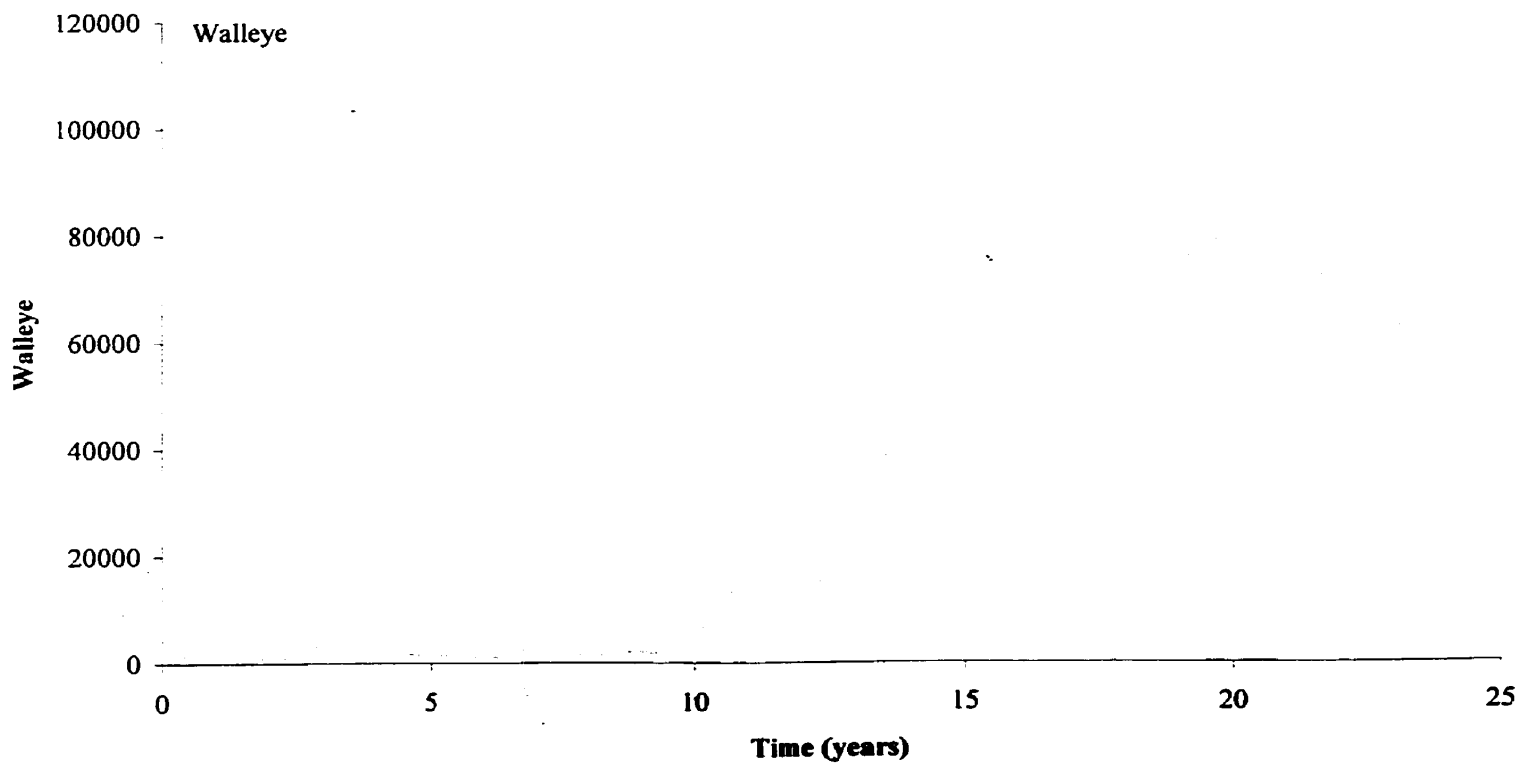
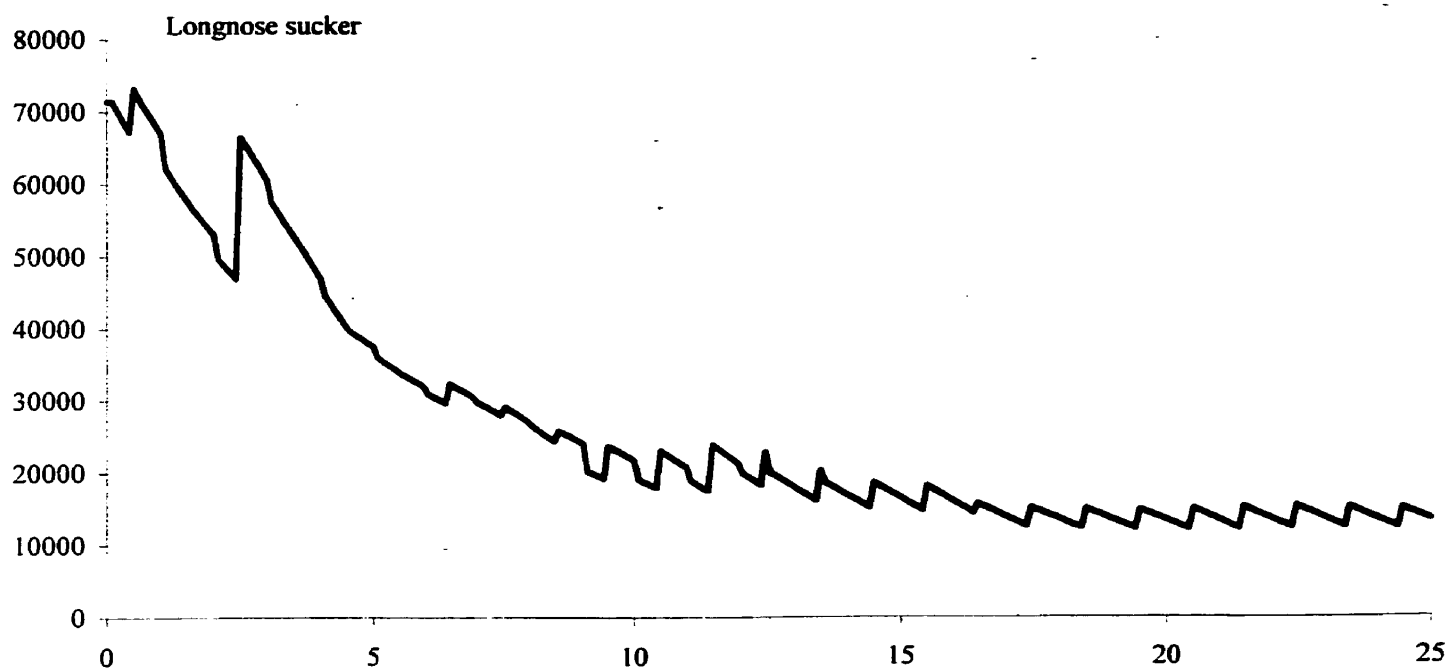


Figure 72. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Alternativ



the Alternative 3 simulation.

subsequently showed a decreasing trend (Figure 72). This was due to an increase in cannibalism which reduced their abundance. The results of this simulation suggest that water level fluctuations during summer may be less important to the fish species included in the model than at other times of the year.

4.4 FISH – Sensitivity Analysis

The purpose of a sensitivity analysis is to learn if the model's general pattern of behaviour is strongly influenced by changes in uncertain parameters. The mechanics of sensitivity testing are simple. Select an individual parameter that is uncertain; change the estimate; and repeat the simulation (Ford 1999). Two types of sensitivity analyses are possible. The first is structural sensitivity where the model user can experiment directly by changing the structure of the model. For example, the number of lifestages in a fishes lifehistory could be changed from seven to six. The second type is simple parameter manipulation of user supplied relationships or coefficients.

The model is capable of estimating and performing an infinite number of sensitivity analyses. An extensive sensitivity testing with the presentation of graphs and results was not included in this thesis, however, was performed by the author. The following generalizations concerning the model's sensitivity were made.

The model appeared to be most sensitive to factors influencing the mortality rates of the egg and larval stages of fish life-history. Significant changes in eggs and larval mortality resulted in large increases or decreases in fish abundance. For example, the availability of zooplankton influenced the larval mortality rate of all fish species included the model. Changes to the abundance of zooplankton dramatically affected results of the model, as an increase or decrease to their relative abundance in the reservoir would alter

results significantly. In comparison with the model's sensitivity to changes affecting the egg and larval stages of fish life-history, all fish included in the model were less sensitive to changes affecting mortality rates of older life stages of fish. As a fish aged, the fish populations became less sensitive to changes in factors that affected their population.

In comparison to the other species included in the model, lake whitefish populations were more sensitive to changes in any one factor affecting their population. Conversely, longnose sucker was most sensitive to water level fluctuations when compared to the other fish species included in the model. Walleye was the fish species most sensitive to changes in their death rate.

For the purposes of this thesis, one sensitivity analyses was included. An example of changing the smelt abundance in the Limestone reservoir is described below.

4.4.1 Smelt 1 (increasing smelt relative abundance)

The affect of increasing rainbow smelt populations in the Limestone reservoir was tested with the Smelt 1 simulation. This simulation involved increasing smelt abundance to maximum relative abundance in the Limestone reservoir, 15 years after impoundment. In general, results suggested that an increased smelt population in the Limestone reservoir would positively effect northern pike and walleye populations, and negatively effect the lake whitefish population, and to a lesser degree, the longnose sucker population (Figure 73). Northern pike numbers were higher relative to Scenario 1 at 26,401, however, a decreasing trend over time was evident (Figure 73). For walleye, this scenario provided the largest numbers of all scenarios presented in this thesis. Walleye numbers increased to 90,434 individuals by the end of the 25 year simulation period (Table 5). Smelt are thought to provide an abundant food source both northern

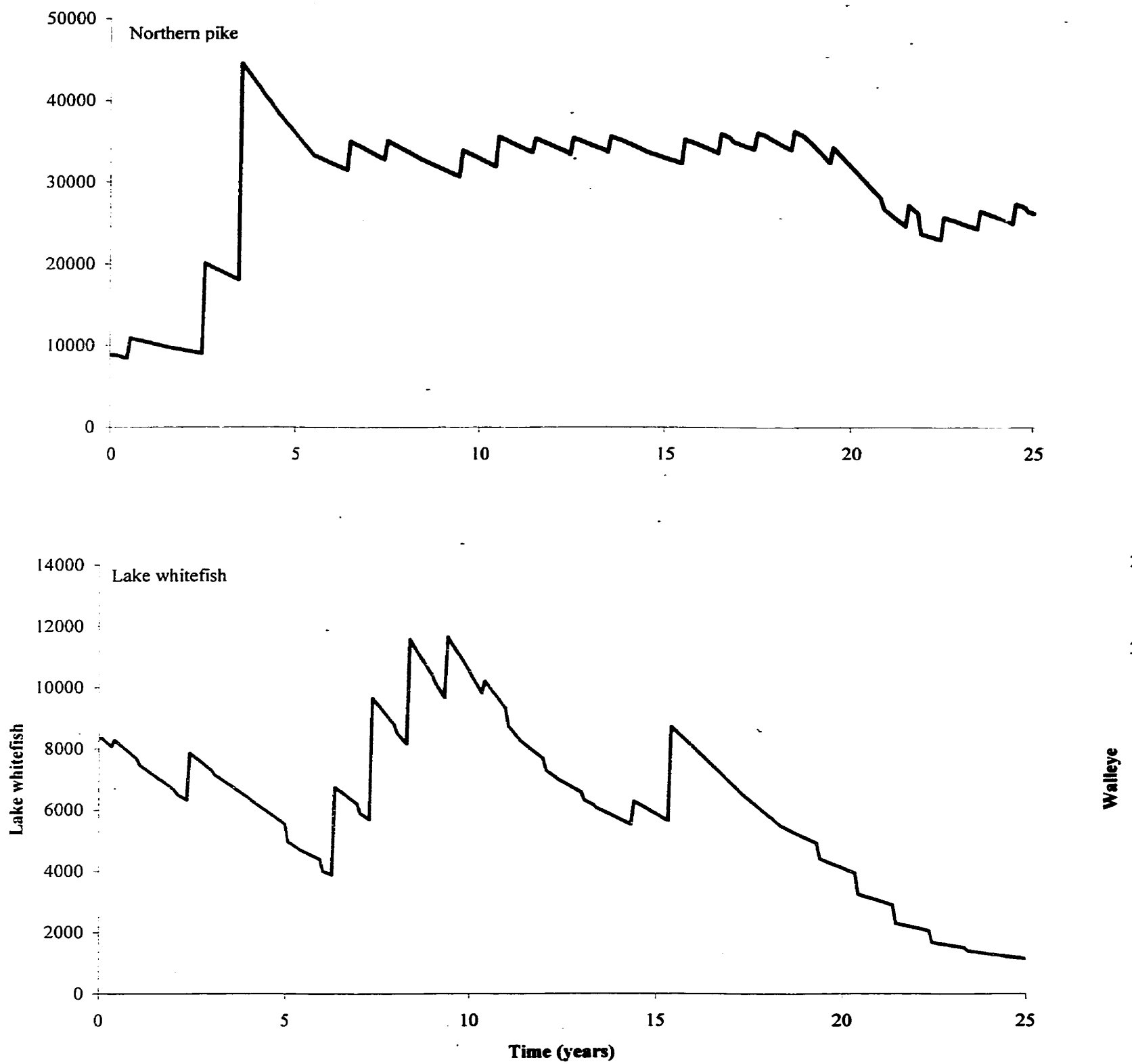
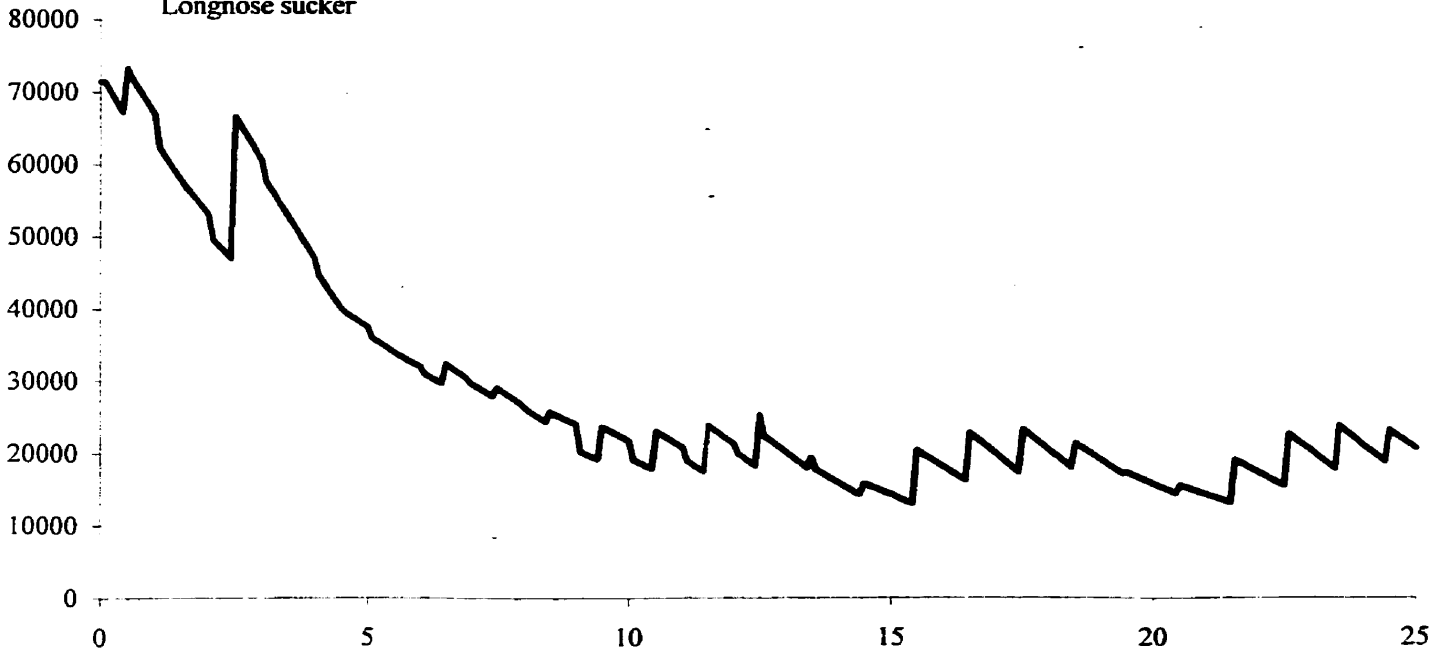
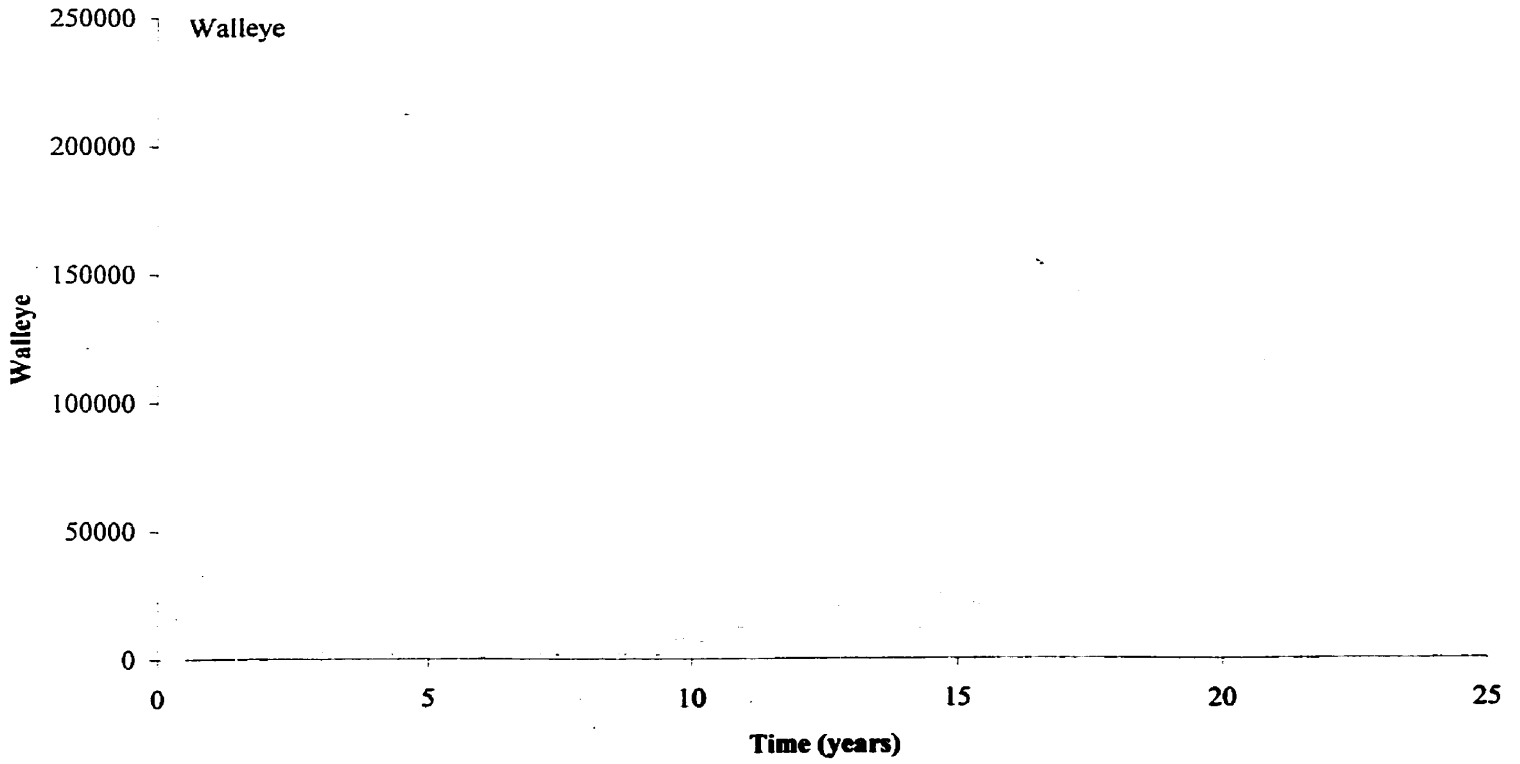


Figure 73. Numbers of northern pike, longnose sucker, lake whitefish and walleye that result from the Smelt simul

Longnose sucker



Walleye



Smelt simulation.

pike and walleye. The increase in predators (northern pike and walleye) resulted in a slight decrease in the longnose sucker population relative to Scenario 1. The longnose sucker population reached 20,552, slightly lower than numbers observed with Scenario 1. Lake whitefish abundance was approximately one-fifth their Scenario 1 numbers (1,158 individuals) (Table 5). This was due not only to an the increase in smelt (smelt have been found to predate upon young lake whitefish), but also due to increased predation from northern pike and walleye populations, both of which increased during this simulation.

CHAPTER 5.0 DISCUSSION

Models are representations of real-world systems. The primary goal of model building is rarely a complete description of reality. Rather, a model simplifies reality effectively to apply existing knowledge towards solving a particular problem. Limitations inherent in modeling include: (a) an incomplete understanding of the real world; (b) a lack of applicable data; (c) a lack of knowledge necessary to describe the real-world problems; and (d) a lack of adequate technology (i.e. computers) for the efficient solution of real-world problems. It is impossible to include all of the interactions that occur in a biological environment, also impossible to have site specific information on all biological interactions and processes. Therefore, when making predictions, we are left to draw upon previous experience and available research. Difficulties occur in defining a starting and ending point for a model, as well as the importance of the interactions included (i.e., too detailed, not enough detail)

At the outset of the research three questions were raised:

1. Can we predict fish abundance in an aging hydroelectric reservoir?

Although it may not be possible to provide a precise estimate of fish numbers, it is possible to identify reservoir conditions that may benefit certain fish species and identify trends in fish abundances under a given set of conditions.

2. Can we make predictions concerning the type of operational strategy that may benefit fish populations in reservoirs?

Previous studies and research has been done on the impacts that reservoir operations have on a reservoir system. The model uses this research to test the impact of a variety of reservoir operations strategies to help predict the impact that a given scenario may have

on fish in a reservoir. This tool can be used to make predictions concerning fish abundance in reservoirs following river impoundment.

3. Can reservoirs be designed or managed to reduce the potential for negative impacts on fish?

Literature and research suggest that a strategy which minimizes water level fluctuations will benefit fish spawning success in a reservoir. Presently, proposed hydroelectric developments in Manitoba are being designed with a water level strategy that minimizes water level fluctuations on a short-term basis. Further research and monitoring on reservoirs operated with year round stable water levels is needed.

5.1 Implications for fish management

Predicting the potential impacts of a proposed or existing hydroelectric developments on fisheries resources is a complex process. Persons evaluating the impacts may be faced with the necessity of making decision even though all of the necessary or desirable information is not available. The tool developed in this research is offered as an aid towards making the “best” decision possible, consistent with the level of knowledge and time available.

Results of the model suggested that reservoir development and hydro operations create conditions that influence fish populations in a variety of ways depending on the nature of the reservoir’s operation. In general, scenarios that reduced short-term water level fluctuations positively affected the abundance of each fish species included in the model. Conversely, scenarios which increased short-term water level fluctuations had adverse effects on fish abundance. Results of the spring flood seasonal operating strategy (i.e., Scenarios 5 to 8) suggested that northern pike benefited from the flooded area each

spring, and their increased abundance increased the predation rates on other fish species included the model.

The alternative scenarios (i.e., Alternatives 1 to 3) indicated that fish species which spawn during spring such as northern pike, longnose sucker and walleye, were more sensitive to water level fluctuations in May (during spawning), and June than during the rest of the year. Fall spawning fish, such as lake whitefish, were more sensitive to water level fluctuations during both their spawning period in November, and their egg incubation period from December through May, than other times of the year. These alternative scenarios suggested that water level fluctuations during late summer and early fall may have less of an impact on the fish species included in the model.

In order to manage hydroelectric reservoirs for increased northern pike populations, Scenario 7, a discharge strategy which flooded area during spring and maintained stable water levels, yielded the highest number (Table 5). Conversely, Scenarios 2 and 6, which increased water level fluctuations, resulted in the lowest numbers of northern pike. The model predicted that the continuation of current operating strategies would result in northern pike populations decreasing over time in the Limestone reservoir. Also, the model predicted that an increase in smelt abundance would benefit northern pike.

To manage hydroelectric reservoirs for lake whitefish, results suggest that a discharge strategy which reduced water level fluctuations during winter, and reduced numbers of northern pike and walleye, would benefit their population. Alternative 2 was found to be the optimal scenario investigated. This strategy reduced water level fluctuations during winter, and did not flood land area in the spring. Conversely, Scenarios 2, 6, and Smelt, had adverse effects on numbers of lake whitefish. These scenarios increased the

magnitude of water level fluctuations (Scenarios 2 and 6), and increased the predation rate on larval lake whitefish (Smelt simulation).

Scientific literature suggests that longnose sucker spawn in shallow water and are very susceptible to water level fluctuations. The optimal discharge strategy was the Scenario 3 simulation, where stable short-term and historical seasonal water level strategies were used. Conversely, Scenarios 2 and 6 which increased water level fluctuations during spring, resulted in poor egg survival and reduced the number of longnose sucker. The model also indicated that Scenarios 5, 6, 7, and 8 which increased the flooded area during spring, negatively affected longnose sucker abundance relative to Scenario 1, 2, 3, and 4, due to the increased abundance of northern pike.

With the exceptions of Scenarios 2 and 6, walleye increased in abundance with all discharge strategies. The optimal discharge strategy for walleye was the Smelt simulation. This was because smelt are thought to provide a valuable food supply for walleye in reservoirs.

Scenario 3 (historical and stable) appeared to benefit each fish species in the model. This Scenario maintained stable water levels for the entire simulation. However, it is important to consider that the **FISH** model could not predict the implications of altered reservoir operations strategies on water quality parameters and biotic components (i.e., zooplankton, invertebrates, forage fish and smelt) of the reservoir ecosystem. Although the model has the capability to investigate the sensitivity of the model to changes in food abundance and water chemistry parameters, these need to be manipulated by the model user, as relationships were not established to automatically simulate the outcomes.

Proposed hydroelectric developments are being planned which would use a reservoir operations strategy similar to Scenario 3. For example, the proposed generating station at Wuskwatim Lake, has been planned to use a water level management strategy that will not fluctuate water levels more than one meter year round. Monitoring the response of fish populations in this reservoir will provide an opportunity to study the changes to water chemistry, invertebrates, fish populations, etc, in a reservoir where stable water levels are maintained. Also, collection of these data will enable comparisons to be made between other reservoirs that utilize different discharge strategies (i.e., reservoirs on the Nelson River, such as Long Spruce and Limestone).

5.2 Limestone reservoir

Machniak (1975c), Petts (1984) and Kimmel and Groeger (1986) among many, discuss that many water quality parameters are related to the lower stages of the food web, (i.e., primary and secondary productivity). With the data that is currently available in the Limestone reservoir (i.e., nutrients, Chlorophyll a) it was identified that many water quality parameters have not changed in response to impoundment. Furthermore, data on lower levels of the food chain were either unavailable from Limestone or indicated that little change has occurred since impoundment. Therefore, it is unclear if forage has become more or less available to fish following development of the Limestone reservoir. There is some evidence to suggest that the availability of food is not limiting fish abundance in the reservoir. Condition factor (measure of fish robustness) could be used to indicate whether the condition of fish was affected by impoundment. However, the condition factor for all fish in the Limestone reservoir has shown little variability

since impoundment. Thus, it seems reasonable to assume that the amount of forage available for fish in the reservoir is not limiting fish abundance in the reservoir.

The data from the monitoring program in the Limestone reservoir, and the model predictions, indicated that fish populations in the Limestone reservoir are still changing 10 years after impoundment. It has been suggested that fish may have completely evolved in response to hydroelectric development 10 years after impoundment (Cooper 1966). The amount of time needed for fish populations to stabilize in response to reservoir development and hydro operations in the Limestone reservoir is unknown. Further data collection would benefit the estimation of this time horizon.

5.3 Data needs

Long-term data sets are necessary to facilitate the development of predictive models and to increase the confidence in the use of predictive models. The lack of long-term quantitative data has been identified as the major problem for both using formal models in fisheries management, and for the development of predictive models (Lackey 1978). The scarcity of quantitative data collected from one reservoir, for five or more consecutive years, is perhaps the greatest hindrance to model development and furthering our overall long-term predictive ability. The data set collected from the Limestone reservoir has been discussed as perhaps being the most complete long-term data set collected for a variety of ecosystem components from any one reservoir in the province. Continued effort to add to the existing data base on a yearly basis should be considered an important objective. Some of the benefits of further data collection include:

- a) an improved ability to make predictions on how fish populations may evolve in the reservoir environment over the long-term;

- b) a further understanding of the response of fish populations to factors that may impact the fish populations in the Limestone reservoir in the future (i.e., smelt); and,
- c) an ability to make comparisons to monitoring data collected from future hydroelectric reservoirs that may use alternate reservoir operations strategies.

One limitation to the development of this model has already been discussed, i.e., the lack of quantitative data concerning the impact that the frequency and amplitude of short-term changes in discharge have on water chemistry and biotic components (i.e., zooplankton) of reservoir ecosystems. The fact that no data were available concerning these potential impacts, however, may be attributed to the difficulty in isolating these factors for scientific analysis. In addition, the amount of data necessary to make accurate conclusions concerning abundance of biotic reservoir components (invertebrates, forage fish, zooplankton) is large. The amount of data required when monitoring these ecosystem components often results in high cost for a properly designed research study. Careful consideration of the methods used to collect these types of data, and the costs associated with this collection, must be given when developing future monitoring programs.

The model suggests that fish may be most sensitive to factors which affect the early stages of their life-history. The effects of discharge rates and water level fluctuations upon the early life history stages may be the critical factor influencing fish production in hydroelectric reservoirs. Collecting information on the spawning locations of certain fish species, collecting estimates on the amount of recruitment to certain fish populations, and estimates of egg survival to changing physical conditions in a reservoir would be useful

information for estimating the potential impacts of the changing physical environment on spawning success.

Interspecies interactions (i.e., predation and competition) are important for modeling fish populations in reservoirs, however, these relationships are difficult to estimate accurately given the best data sets. Continued collection of fish stomachs from the Limestone reservoir would provide an indication of how diet was changed over time, and provide a basis for which to estimate predation rates. Future research may improve our ability to quantify such interactions.

Although data from the Limestone reservoir indicates that smelt are increasing in abundance, it is uncertain to what extent their populations will become established in the reservoir, or how their population affects the native fish species in the Limestone reservoir. Since smelt have been shown to impact fish populations in other lakes and reservoirs, future monitoring of the Limestone reservoir should consider smelt as an important ecosystem component to monitor. With the data set that has currently been collected in the Limestone reservoir, further monitoring will enable an opportunity to study the impact that smelt colonization has on fish species in a northern hydroelectric reservoir.

5.4 Further use/applications

At the outset of this study it was anticipated that the model could be re-applied to any hydroelectric reservoir. However, the degree of alteration of downstream flow patterns can vary considerably among projects, and is a complex function of the project design and the watershed characteristics. As a result, the physical characteristic data (i.e., stage storage curve, area, depth, etc) used to derive the relationships inputted into

HYDRAULIC and **FISH** are specific to the Limestone reservoir and cannot be re-applied to another reservoir. Application of these models to other reservoir systems would require the model user to input physical data into the model framework. The overall framework of the model, the literature that was used as a basis for various relationships, and methods used to develop the model, may be used when applying to another reservoir.

Two future uses of the **HYDRAULIC** model are possible. The first concerns investigating and predicting site specific changes to fish habitat that may result from reservoir development and alternative reservoir operations strategies. Manitoba Hydro generally collects cross-sectional data prior to the development of hydroelectric sites. Application of a model such as **HYDRAULIC**, to the planning phase of a development, would allow for changes to fish habitat resulting from changes in water level and discharge strategy to be evaluated prior to construction. For example, if a valuable lake whitefish spawning location is known prior to hydroelectric development, cross-sectional data could be built into a model to investigate both the impact in water level, and changes in discharge rate may have on the physical characteristics on this specific spawning area.

A second potential future use of **HYDRAULIC** is to further develop the model such that it can explore the impacts that short-term changes in discharge may have on biota of the reservoir. As discussed in Chapter 2, scientific literature discussing the impacts that short-term variations in discharge have on aquatic biota is scarce in Canadian waters. The **HYDRAULIC** model could be further developed and used to test alternative hypothesis.

Future applications of the **FISH** model should include further testing alternative hypotheses, discussion of model inputs and results, and building upon the existing model framework. The model could be used by developers, engineers and biologists to test the impact of various reservoir management strategies on fish populations. Future use of the model would also allow for the incorporation of new data. Furthermore, models are currently being developed for Manitoba Hydro to predict the outcomes of various management alternatives for power generation and mercury estimation in new and existing impoundment. This model fits in as a component with other models that have and are currently being developed for Manitoba Hydro.

Before use on another system, further review, testing and discussion of this model should be completed. This is a new application of a computer simulation model to a hydroelectric reservoir. Future research and review should be conducted to increase the confidence in this model and its use and application to other systems.

5.4 Summary

The model structure provides a framework upon which an investigator can build on and experiment with the hydro discharge strategies or population parameters of a fish population. The framework is flexible and easy to change both input data and relationships. In order to apply the model framework another reservoir, or use the model with existing information, some time is necessary to become familiar with its requirements. Additional time is required to obtain the data from the system, input the system data into the model, adjust parameters, and do preliminary trials to observe if the simulation performed realistically. However, once this has been completed, countless experiments on fish populations in reservoirs can be conducted. The applications of this

tool are numerous. It can provide a means of allowing interested parties to test hypotheses and alternative management scenarios. At the very least it provides a tool that can provide biologists, developers and regulators a better understanding of the factors influencing these four fish populations in an aging hydroelectric reservoir.

Two models were developed by this research. These included the **HYDRAULIC** model, which accurately predicted changes to the physical reservoir environment, and the **FISH** model, which allowed for alternative reservoir operations strategies to be tested on four species of fish. Development of the **FISH** model showed that physical-biological, chemical-biological and biological-biological interactions were difficult to quantify and could not be estimated or measured with the same degree of precision and accuracy as physical characteristics of the environment, simulated by the **HYDRAULIC** model. Therefore, it can be stated that we can accurately predict changes to the physical environment following reservoir development, but chemical-biological and biological-biological interactions are often poorly understood and difficult to quantify.

The goal of the **FISH** model was to capture the trends observed in fish populations following impoundment, rather than providing a precise estimate of fish numbers in the reservoir. Achieving a precise representation of the number of fish in a reservoir with a model is an impossible objective to achieve at the present time, due to the lack of site specific data, and due to difficulties in predicting the impacts of factors beyond human control (i.e., weather). The trends observed in Figures 62 - 73 are more important than the actual numbers provided in Table 5 of the results section.

6.0 Conclusions and Recommendations

6.1 Conclusions

1. This research has been offered as a first step towards: (a) predicting fish abundance in an aging hydroelectric reservoir; and (b) analyzing the impact of alternative discharge strategies on fish populations within hydroelectric reservoirs.
2. The model framework should be used as a building block for future modeling efforts and used to provide decision makers with a tool to help assess how fish populations are affected by hydro development and reservoir operations.
3. This model can be used as an aid for testing hypotheses, making decisions during the early stages of project planning, and/or for assessing potential impacts of changing current operations.
4. Models developed to represent biological systems cannot be precise representations of the actual system due to our limited understanding of interactions in the environment and our inability to predict or control certain conditions (i.e., weather). The greatest accuracy that can be achieved is a representation of trends or magnitude of change. For example the fish population trends observed in Figures 62-73 are more important than the actual numbers provided in Table 5.
5. The model works as a component with other models which have been, or are currently being, developed for Manitoba Hydro.
6. The ability to predict how the physical environment will change as a result of hydroelectric development has been well developed and can be done

accurately. For example, the **HYDRAULIC** model is capable of testing how hourly discharge rates impact the physical reservoir environment.

7. The model predicts that a reservoir operations strategy that reduces water level fluctuations may benefit fish populations in hydroelectric reservoirs.
8. The impact of maintained stable water levels on the aquatic reservoir environment needs further study.
9. In general, each fish population included in the model was most sensitive to factors which influence the survival of the egg and larval life-stages of fish populations. Fish abundance in reservoirs may be highly dependant upon the survival of these life-phases.

6.2 Recommendations

1. Further testing, research and discussion of the model and model framework would be useful to improve existing relationships, build on the existing model, and test additional hypotheses.
2. Application of the model framework to a proposed hydroelectric development should be considered.
3. Scientific work should be done on the impacts that reservoir operations may have on the egg and larval life-stages of fish life-history. The model indicates that survival of these young life-stages may be a critical influence on fish populations in hydroelectric reservoirs.

6.2.1 Limestone reservoir

1. Continued monitoring of the Limestone reservoir in order to add to the existing data base should be considered. Further data collection would enable

comparisons to be made between the Limestone reservoir, and other reservoirs, which may be regulated differently.

2. Future data collection should focus on the impact that discharge fluctuations may have on water chemistry and primary and secondary productivity of the reservoir environment. For example, the impact of a maintained stable water level year round in a reservoir system requires further study.
3. The relationship between fish growth and reservoir development should be investigated for not only the Limestone reservoir, but other reservoirs in Manitoba.

7.0 Literature Cited

- Alberto, J., J. R. Stedinger, and K. Staschus. 1990. Optimization of value of CVP's hydropower production. *Journal of Water Resources Management*. Vol. 116. No. 1. 52-69p.
- Allen, K. R. 1939. A note on the food of the pike (*Esox lucius*) in Windermere. *J. Anim. Ecol.* 8:72-75.
- Anderson, E. D., and L. L. Smith. 1971. Factors affecting abundance of lake herring (*Coregonus artedii*) in Western Lake Superior. *Trans. Am. Fish. Soc.* 100(4):691-707.
- Axelsson, J. 1961. Zooplankton and impoundment of two lakes in Northern Sweden. *Rept. Inst. Freshwater Res. Drottninghom.* 42:84-168.
- Baker, R. F., D. S. MacDonell, and S. Davies. 1990. A fisheries survey of the Long Spruce Forebay. A report prepared for Manitoba Hydro by North/South Consultants Inc. 55p.
- Baker, R. F. 1990. A fisheries survey of the Limestone Forebay, 1989 – Year I. A report prepared for Manitoba Hydro by North/South Consultants Inc. 66p.
- Baker, R. F. and S. Davies. 1991. Physical, Chemical, and Biological Effects of the Churchill River Diversion and Lake Winnipeg Regulation on Aquatic Ecosystems. *Can. Tech. Rep. Fish. Aquat. Sci.* no. 1806. 53p.
- Baker, R. F. and F. Schneider-Vierra. 1993. Development of the insect fauna in the Limestone Forebay following impoundment and comparison with undisturbed sites at the Long Spruce Forebay and the Lower Nelson River Mainstem. A report prepared for Manitoba Hydro by North/South Consultants Inc. 35p.

- Barton, B. A. 1980. Spawning migrations, age and growth and summer feeding of white and longnose suckers in an irrigation reservoir. *Can. Field-Nat.* 94(3):300-304.
- Baxter, R. M. 1977. Environmental Effects of Dams and Impoundments. *Ann. Rev. Ecol. Syst.* Vol. 8:255-283.
- Baxter, R. M. and P. Glaude. 1980. Environmental effects of dam and impoundments in Canada: Experience and Prospects. *Can. Bull. Fish. Aquat. Sci.* no. 205. 34p.
- Benson, N. G. 1980. Effects of post-impoundment shore modifications of fish populations in Missouri River reservoirs. *U.S. Fish. Wildl. Serv. Rep.* 80:32.
- Bergazzi, P. R., and C. R. Kennedy. 1980. The biology of the pike, *Esox lucius* in a southern eutrophic lake. *J. Fish. Biol.* 17:91-112.
- Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited populations of lake whitefish (*Coregonus clupeaformis*). *J. Fish. Res. Bd. Can.* 34:942-953.
- Beyerle, G. B., and J. E. Williams. 1968. Some observation of food selectivity by northern pike in aquaria. *Trans. Am. Fish. Soc.* 97(1):28-31.
- Bietz, B. F., J. Grant, and P. McKee. 1988. Stock-Habitat relationships for selected Canadian freshwater fish. Prepared for the Canadian Electrical Association by Beak Associates Consulting, Edmonton Alberta. 137p.
- Bodaly, R. A., T. W. Johnson, R. J. P. Fudge, and J. W. Clayton. 1984(a). Collapse of the lake whitefish (*Coregonus clupeaformis*) fishery in Southern Indian Lake, Manitoba, following lake impoundment and river diversion. *Can. J. Fish. Aquat. Sci.* 41:692-700.

- Bodaly, R. A., D. M. Rosenberg, M.N. Gaboury, R. E. Hecky, R. W. Newbury, and K. Patalas. 1984(b). Ecological effects of hydroelectric development in Northern Manitoba, Canada: The Churchill-Nelson River diversion, p273-309. In: P. J. Sheehan, D. R. Miller, G. C. Butler and Ph. Bourdeau (ed.) Effects of pollutants at the ecosystem level. John Wiley and Sons Ltd., Chichester, UK.
- Bodaly, R. A., and L. F. W. Lesack. 1984. Response of a boreal northern pike (*Esox lucius*) population to lake impoundment: Wupaw Bay, Southern Indian Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41(5):706-714.
- Bretecher, R. L. and B. D. Home. 1997. Lower Nelson River monitoring program 1996. A report prepared for Manitoba Hydro by North/south Consultants Inc. 71p.
- Bretecher, R. L. and D.S. MacDonell. 1998. Lower Nelson River Forebay monitoring program. A report prepared for Manitoba Hydro by North/South Consultants Inc. 37p.
- Bretecher, R. L. and D. S. MacDonell. 1999. Lower Nelson River Forebay monitoring program. A report prepared for Manitoba Hydro by North/South Consultants Inc.
- Bretecher, R. L. and D. S. MacDonell. 2000. Lower Nelson River Forebay monitoring program. A report prepared for Manitoba Hydro by North/South Consultants Inc.
- Bridges, C. H., and L. S. Hambly. 1971. A summary of eighteen years of salmonid management at Quabbin Reservoir, Massachusetts. Am. Fish. Soc. Spec. Publ. 8:243-259.
- Brown, C. D., and R. J. Graham. 1953. Observations on the longnose sucker in Yellowstone Lake. Trans. Am. Fish. Soc. 83:38-46.

- Brown, R. W. and W. W. Taylor. 1992. Effects of egg composition and prey density on the larval growth and survival of lake whitefish (*Coregonus clupeaformis*). J. Fish. Biol. 40:381-394.
- Bryan, S. D., T. D. Hill, S. T. Lynott, and W. G. Duffy. 1995. The influence of changing water levels and temperatures on the food habits of walleye in Lake Oahe, South Dakota. J. Fresh. Wat. Ecol. 10(1):1-10.
- Campbell, K. B., A. J. Derksen, R. A. Remnant, and K. W. Stewart. 1991. First specimens of the rainbow smelt, *Osmerus mordax*, from Lake Winnipeg, Manitoba. Can. Field Nat. 105(4):568-570.
- Carbine, W. F. 1938. The pike: a prized and spurned fish. Mich. Conserv. 7:6-8.
- Carbine, W. F. 1942. Observations on the early life history of the northern pike, *Esox lucius*, in Houghton Lake, Michigan. Trans. Am. Fish. Soc. 71:149-164.
- Casselman, J. M., and C. A. Lewis. 1996. Habitat requirements of Northern pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. 53(Suppl 1): 161-174.
- Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Trans. Am. Fish. Soc. 102:739-744.
- Christie, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Bd. Can. 27:1875-1879.
- Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Bd. Can. 31:827-854.
- Clark, C. F. 1950. Observation on the spawning habits of northern pike, *Esox lucius*, in northwestern Ohio. Copeia 1950(4) : 258-288.

- Cohen, Y., and P. Radomski. 1993. Water level regulations and fisheries in Rainy Lake and the Namakan Reservoir. *Can. J. Fish. Aquat. Sci.* 50: 1934-1945.
- Colby, P. J., P. A. Ryan, D. H. Schupp and S. L. Serns. 1987. Interactions in north-temperate lake fish communities. *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2): 104-128.
- Cook, M. F. and E. P. Bergsen. 1988. Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Trans. Am. Fish. Soc.* 117:495-502.
- Cooper, G. P. 1966. Fish production in impoundments. Mich. Dept. Conserv., Res. Dev. Rept. 104:21pp.
- Cooper, J. L. 1971. The northern pike in Fort Peck Reservoir, Montana. *Pro. Montana Acad. Sci.* 31:53-61.
- Crawford, D. R. 1923. The significance of food supply in the larval development of fishes. *Ecology* 4:147-153.
- Crowder, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? *Envir. Biol. Fishes* 5:225-233.
- Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *N. Am. J. Fish. Manag.* 5:330-339.
- Cushing, D. H. 1974. The possible density-dependence of larval mortality and adult mortality in fishes, p. 103-111. In J. H. S. Blaxter. *The early life history of fish.* Springer-Verlag, New York, New York.
- Cushing, D. H. 1988. The study of stock and recruitment. Pages 105-128 in J. A. Gulland (Ed). *Fish population dynamics*, 2nd edition. Wiley, New York.

- DeAngelis, D. L., S. W. Christensen, and A. G. Clark. 1977. Responses of a fish population model to young-of-the-year mortality. J. Fish. Res. Bd. Can. 34:2124-2132.
- Deriso, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37:268-282.
- Derksen, A. J. 1967. Variations in abundance of walleye, *Stizostedion vitreum*, in Cedar Lake and Moose Lakes, Man. M. S. Thesis, Univ. Man., Winnipeg, Man. 98p.
- DesLandes, J., S. Guenette, and R. Fortin. 1994. Summary report: Evolution of fish communities in environments affected by the development of the La Grande Complex, Phase I (1992-1997). Hydro-Quebec. 74p.
- Diana, J. S. 1983. Growth, Maturation, and Production of Northern pike in three Michigan Lakes. Trans. Am. Fish. Soc. 112:38-46.
- Doan, K. H. 1979. Commercial catch of the fishery at Cedar Lake, Manitoba, before and after the Grand Rapids hydroelectric project. MS Rep. No. 79-48. 28pp.
- Edwards, E. A. 1983. Habitat suitability index models: Longnose sucker. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.35. 21p.
- Enfalt, L. M. and D. H. Wahl. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behaviour. Can. J. Fish. Aquat. Sci. 54:2618-2626.
- Erickson, J. 1972. Evaluation of environmental factors of Ohio reservoirs in relation to the success of walleye stocking. Ohio Dept. Nat. Res., Fed. Aid. Fish. Wildl. Restor. Proj. Job No. 9:21p

- Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. *Can. J. Fish. Aquat. Sci.* 44(suppl. 2):249-266.
- Evans, D. O., and P. Waring. 1987. Changes in the multi-species, winter angling fishery of Lake Simcoe, Ontario, 1961-83: invasion by rainbow smelt *Osmerus mordax*, and the role of intra-and inter-specific interactions. *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2):182-197.
- Farmer, A. H., M. J. Armbruster, J. W. Terrell, and R. L. Schroeder. 1982. Habitat models for land use planning: Assumptions and strategies for development. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 47:47-56.
- Fisher, S. G., and A. LaVoy. 1972. Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. *J. Fish. Res. Bd. Can.* 29:1472-1476.
- Fletcher, E. J. 1998. The use of system dynamics as a decision support tool for the management of scarce water resources. Conference on New Technologies and Decision Making in Civil Engineering. Montreal, Canada. 909-921.
- Ford, A. 1999. Modeling the Environment – An introduction to System Dynamics Modeling of Environmental Systems. Island Press. Washington. D. C. 401p.
- Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum*) population of Oneida Lake, New York, 1966-73. *J. Fish. Res. Bd. Can.* 33:783-792.
- Forrester, J. W. 1961. Industrial Dynamics. Productivity Press. Portland, Oregon. 464pp.
- Fraser, J. C. 1972. Regulated discharge and the stream environment. Pp. 26-85 in *River Ecology and Man*. Academic Press, New York: 465p.

- Freeberg, M. H., Taylor, W. W. and R. W. Brown. 1990. Effect of egg and larval survival on the year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. *Trans. Am. Fish. Soc.* 119:92-100.
- Frost, W. E. 1954. The food of the pike, *Esox lucius*, in Windermere. *J. Anim. Ecol.* 23:339-360.
- Frost, W. E., and C. Kipling. 1967. A study of reproduction, early life, weight length relationship and growth of pike, *Esox lucius*, in Windermere. *J. Anim. Ecol.* 36:651-693.
- Fudge, R. J. P. and R. A. Bodaly. 1984. Post-impoundment winter sedimentation and survival of lake whitefish (*Coregonus clupeaformis*) eggs in Southern Indian Lake. *Can. J. Fish. Aquat. Sci.* 41:701-705.
- Gaboury, M. N. and J. W. Patalas. 1984. Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. *Can. J. Fish. Aquat. Sci.* 41:118-125.
- Giberson, D. J., D. M. Rosenberg, and A. P. Wiens. 1992. Long-term abundance patterns of *Hexagenia* in Southern Indian Lake, Manitoba: responses to weather and hydroelectric development. *Can. Tech. Rep. Fish. Aquat. Sci.* 1837:iv +16p.
- Giberson, D. J. and D. M. Rosenberg. 1994. Life histories of burrowing mayflies (*Hexagenia limbata* and *H. rigida*, *Ephemeroptera: Ephemeridae*) in a Northern Canadian reservoir. *Freshwater Biology*: 32: 501-518.
- Gorodinichii, A. E. 1971. Methods of improving the natural spawning grounds of semi-migratory fish on the Don River. *J. Hydrobiol.* 7(4):40-44.
- Grimm, M. P. 1981. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius*). *Fish. Manage.* 12(2):77-79.

- Groen, C. L. and T. A. Schroeder. 1978. Effects of water level management on walleye and other coolwater fishes in Kansas Reservoirs. In: Selected cool-water fishes of North America, A. Fish. Soc. Spec. Publ. 11:278-283.
- Hales, Z. L., A. Shindala, and K. H. Denson. 1970. Riverbed degradation prediction. Water Resources Research 6:549-56.
- Hannon, B. and M. Ruth. 1997. Modeling Biological Systems. Springer-Verlag. New York. 399p.
- Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958-1996. North American Journal of Fisheries Management. 18:764-774.
- Hart, J. L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis*, in the Bay of Quinte, Ontario. Ph.D. Thesis, Univ. Toronto.
- Hartman, W. L. 1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fish. Comm. Tech. Rept. 22:43pp.
- Hassler, T. J. 1970. Environmental influences on early development and year-class strength of northern pike in Lake Oahe and Sharpe, South Dakota. Trans. Am. Fish. Soc. 99:369-375.
- Hecky, R. E., R. W. Newbury, R. A. Bodaly, K. Patalas, and D. M. Rosenberg. 1984. Environmental prediction and assessment: the Southern Indian Lake experience. Can. J. Fish. Aquat. Sci. 41:720-732.
- High Performance Systems. 1992. Getting started with STELLA II: A Hands-On Experience. High Performance Systems, Inc. Hanover, NH. 196p.

- High Performance Systems. 1994. STELLA II. An introduction to systems thinking. High Performance Systems Inc. Hanover, NH. 96p.
- Holcik, J. 1968. Freshwater Fishes. The Hamlyn Publishing Group Ltd. 128p.
- Holland, L. E., and M. L. Huston. 1984. Relationship of young of the year northern pike to aquatic vegetation types in backwaters of the upper Mississippi River. N. Am. J. Fish. Manage. 4:514-522.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist. 91:385-398.
- Horne, B. D. and R. F. Baker. 1993. A fisheries survey of the Limestone forebay 1992 – year IV. A report prepared for Manitoba Hydro by North/South Consultants Inc. 48p.
- Horne, B. D. 1995. Lower Nelson River Forebay monitoring program. 1994 – Year VI. A report prepared for Manitoba Hydro by North/South Consultants Inc. 40p.
- Horne, B.D. 1996. Lower Nelson River Forebay monitoring program 1995 – Year VII. A report prepared for Manitoba Hydro by North/South Consultants Inc. 48p.
- Hunt, B. P., and W. F. Carbine. 1951. Food of young pike, *Esox lucius* and associated fishes in Peterson's ditches, Houghton Lake, Michigan. Trans. Am. Fish. Soc. 80:67-83.
- Il'ina, L. K., and N. A. Gordeev. 1970. Dynamics of the reproductive conditions of phytophilous fishes at different stages in reservoir formation. J. Ichthyol. 10(3): 282-285.
- Il'ina, L. K., and N. A. Gordeev. 1972. Water-level regime and the spawning of fish stocks in reservoirs. J. Ichthyol. 12(3):373-381.

- Inskip, P. D. 1982. Habitat suitability index models: Northern pike. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.17. 40p.
- Jenkins, R. M. 1970. The influence of engineering design and operation and other environmental factors on reservoir fishery resources. *Water Resource Bull.* 6:110-118.
- Jensen, A. J. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis*. *J. Fish. Biol.* 19: 557-573.
- Jensen, A. J. 1985. Relations among net reproductive rate and Life history parameters for lake whitefish (*Coregonus clupeaformis*). *Can. J. Fish. Aquat. Sci.* 42: 164-168.
- Jensen, A. J. 1989. Simulation of the potential for life history components to regulate walleye population size. *Ecol. Modeling*, 45: 27-41.
- Jonas, J. L., and D. H. Wahl. 1998. Relative importance of direct and indirect effects of starvation for young walleyes. *Trans. Am. Fish. Soc.* 127:192-205.
- Johnson, F. H. 1957. Northern pike year-class strength and spring water levels. *Trans. Am. Fish. Soc.* 86:285-293.
- Johnson, F. H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. *Trans. Am. Fish. Soc.* 90:312-322.
- Jones, M.S., J. P. Goettl, and S. A. Flicklinger. 1994. Changes in walleye food habits and growth following a rainbow smelt introduction. *N. Am. J. Fish. Manage.* 14:409-414.
- June, F. C. 1970. Atresia and year-class abundance of northern pike *Esox lucius*, in two Missouri River impoundments. *J. Fish. Res. Bd. Can.* 27:587-591.

- June, F. C. 1976. Changes in young-of –the-year fish stocks during and after filling of Lake Oahe, an upper Missouri River storage reservoir, 1966-74. U.S. Dept. Int., Fish Wild. Serv. Tech. Pap. 87. 25p.
- Kimmel B. L. and A. W. Groeger. 1986. Limnological and ecological changes associated with reservoir aging. In: Reservoir fisheries management: Strategies for the 80's. Bethesda, Maryland. p103-109.
- Knight, W. 1969. A formulation of the von Bertalanffy growth curve when the growth rate is roughly constant. Journal of the Fisheries Research Board of Canada. 16:3069-3072.
- Knight, R. L., Margraf, F. J., and Carline, R. F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. 113:677-693.
- Knight, R. L., and B. Vondracek. 1993. Changes in prey fish populations in western Lake Erie, 1969-88, as related to walleye, *Stizostedion vitreum*, predation. Can. J. Fish. Aquat. Sci. 50: 1289-1298.
- Kupchinskaya, E.S. 1985. Pike, *Esox lucius*, of Ust-Ilimskoe Reservoir. J. Ichthyol. 25(1): 133-141.
- Kuznetsov, V. A. 1980. Fluctuation in the abundance of commercial fishes influenced by regulated river discharge (as exemplified by Kuybyshev Reservoir). J. Ichthyol. 20(5):32-37.
- Lackey, R. T. 1978. Fisheries Management Theory. In: Selected cool-water fishes of North America. Am. Fish. Soc. Spec. Publ. 11:417-423.

- Lawrence, M. J., C. R. Fazakas, L. Zrum, C. L. Bezte, and W. J. Bernhardt. 1999. The Split Lake Aquatic Ecosystem. A synthesis of Split Lake Biological and Environmental data. January 1997 – October 1998. A report prepared by North/South Consultants for the Tataskweyak Environmental Monitoring Agency.
- Lawler, G. H. 1961. Egg counts of Lake Erie whitefish. J. Fish. Res. Bd. Can. 18:293-294.
- Lawler, G. H. 1965. The food of the pike, *Esox lucius*, in Heming Lake, Manitoba. J. Fish. Res. Bd. Can. 22:1357-1377.
- Loftus, D. H., and P. F. Hulsman. 1986. Predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedii*) by adult rainbow smelt (*Osmerus mordax*). Can. J. Fish. Aquat. Sci. 43:812-818.
- Lowe-McConnell, R. H. 1973. Reservoirs in relation to man-Fisheries. In: Ackerman, W. C. et al. (Eds.) 1973. Man-Mad Lakes: Their problems and Environmental Effects. Geophys. Monogr. Ser., Vol. 17:641-654.
- Lyons, J. and J. J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Trans. Am. Fish. Soc. 116:29-39.
- Macan, T. T. 1963. Freshwater Ecology. Longmans, London, England. John and Wiley, New York, USA: 338p.
- MacDonell and B. D. Horne. 1994. Lower Nelson River Forebay monitoring program 1993 – year V. a report prepared for Manitoba Hydro by North/South Consultants Inc. 111p.

- Machniak, K. 1975(a). The effects of hydroelectric development on the biology of northern fishes, (reproduction and population dynamics) northern pike. Can. Tech. Rep. Fish. Aquat. Sci. no. 528. 82p.
- Machniak, K. 1975(b). The effects of hydroelectric development on the biology of northern fishes, (reproduction and population dynamics) lake whitefish. Can. Tech. Rep. Fish. Aquat. Sci. no. 527. 67p.
- Machniak, K. 1975(c). The effects of hydroelectric development on the biology of northern fishes (reproduction and population dynamics) yellow walleye. Can. Tech. Rep. Fish. Aquat. Sci. no. 529. 30p.
- MacLaren Plansearch Inc/Intergroup Consultants Inc. 1986. Limestone Generating Station environmental impact study: Final report. A report prepared for Manitoba Hydro by MacLaren/InterGroup. 165p.
- Manitoba Hydro. 1995. The hydro province. Manitoba Hydro. Winnipeg, Manitoba. Canada.
- Masse, G., Dumont, P., and Fortin, R. 1993. Survie oeufs-juveniles et force des classes d'age des grand brochets (*Esox lucius*) de la riviere aux pins, pres de Montreal, Quebec. Can. J. Zool. 71:368-375.
- May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. p. 3-20. In J. H. S. Blaxter. The early life history of fish. Springer-Verlag, New York, New York.
- McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fish of northwestern Canada and Alaska. Fish. Res. Bd. Can. 22:1357-1377.

- Miller, R. B. 1952. The relative strength of whitefish year classes as affected by egg planting and weather. *J. Wildlife. Mgmt.* 16:39-49.
- Morrow, J. W., G. L. Miller, and K. J. Killgore. 1997. Density, size and foods of larval northern pike in natural and artificial wetlands. *N. Am. J. Fish. Manage.* 17:210-214.
- Nelson, W. R. 1978. Implication of water management in Lake Oahe for the spawning success of cool-water fishes. *Am. Fish. Soc. Spec. Publ.* 11:154-158.
- Nester, R. T. and T. P. Poe. 1984. Predation on lake whitefish eggs by longnose suckers. *J. Great Lakes Res.* 10(3):327-328.
- Nielsen, L. A. 1980. Effect of walleye (*Stizostedion vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* 37:11-19.
- Niemuth, W., W. Churchill, and T. Wirth. 1959. The walleye, its life history, ecology and management. *Wis. Dept. Nat. Res., publ. No. 227: 14p.*
- Orth, D. J. 1975. Development of a computer simulation model of largemouth bass population dynamics. Master's thesis, Oklahoma State University, Stillwater, Oklahoma, USA.
- Ossimitz, G. 1998. The development of systems thinking skills using system dynamics modeling tools. Available
@<http://www.uni-klu.ac.at/users/gossimit/eng/sdyneng.html> (Mar. 1999).
- Parsons, J. W. 1971. Selective food preferences of walleyes in the 1959 year class in Lake Erie. *Trans. Am. Fish. Soc.* 100:474-485.

- Paulik, G. J. 1969. Computer simulation models for fisheries research, management and teaching. *Trans. Am. Fish. Soc.* 98:551-559.
- Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock-production model. *Inter-American Tropical Tuna Commission [Bulletin]* 1:27-56.
- Penner, F., D. Sie, H. Henderson and P. Ould. 1975. Lower Nelson River study: river geomorphology and timber clearing. Department of Mines, Resources and Environmental Management, Water Resources Division. 276p.
- Petts, G. E. 1984. Impounded rivers. John Wiley and Sons Ltd. London, England. 325p.
- Petts, G. E., P. Armitage, and E. Castella. 1993. Physical habitat changes and macroinvertebrate response to river regulation. *Reg. Riv. Res. Manag.* Vol. 8(8) 13-19.
- Playle, R. C. and D. A. Williamson. 1986. Water chemistry changes associated with hydroelectric development in Northern Manitoba: the Churchill, Rat, Burntwood, and Nelson Rivers. *Water Standards and Studies Report no.* 86-8. 50p.
- Plosky, G. R. 1986. A review of the effects of water-level changes on reservoir fisheries and recommendations for improved management. In: *Reservoir fisheries management – strategies for the 80's*. American Fisheries Society. 86-97p.
- Prentice, J. A. and R. D. Clark. 1978. Walleye fishery management program in Texas – a systems approach. *Trans. Am. Fish. Soc. Spec. Publ.* 11:408-416.
- Priegel, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. *Wis. Dept. Nat. Res., Tech. Bull. No.* 45: 105p.

- Radzicki, M. 1997. A system dynamics analysis of restructuring New York State electric power industry. Available
@<http://www.ce.umanitoba.ca/~simon/56721/56721.html> (Oct. 1998).
- Rawson, D. S., and C. A. Elsey. 1948. Reduction in longnose sucker population of Pyramid Lake, Alberta, in an attempt to improve angling. Trans. Am. Fish. Soc. 78:13-31.
- Regier, H. A., V. C. Applegate, and R. A. Ryder. 1969. The ecology and management of the walleye (*Stizostedion vitreum*) in western Lake Erie. Great Lakes Fish. Comm., Tech. Rep. 15:101p
- Reckahn, J. A. 1970. Ecology of young lake whitefish (*Coregonus clupeaformis*) in South Bay, Manitoulin Island, Lake Huron. In: C. C. Lindsey and C. S. Woods (Eds.). Biology of Coregonid fishes: 437-460.
- Remnant, R. A. 1991. An assessment of the potential impact of the rainbow smelt on the fishery resources of Lake Winnipeg. Unpublished MNRM practicum, University of Manitoba, Winnipeg, MB. 170p.
- Remnant, R. A., P. G. Graveline., and R. L. Bretecher. 1997. Range extension of the rainbow smelt (*Osmerus Mordax*), in the Hudson Bay drainage of Manitoba. Can. Field. Nat. 111(4):660-662.
- Richardson, G. P. 1986. Problems with causal-loop diagrams. System Dynamics Review 2 (no. 2, Summer 1986) 158-170.
- Richmond, B. 1993. Systems thinking: critical thinking skills for the 1990's and beyond. In: System Dynamics Review, Vol. 9, no. 2 (Summer 1993):113-133.

- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Bd. Can. Bull.* 191:382 p.
- Ritchie, B. J., and P. J. Colby. 1988. Even-odd year differences in walleye year-class strength related to mayfly production. *N. Am. J. Fish. Manage.* 8:210-215.
- Rosenberg, D.M., R. A. Bodaly, R. E. Hecky, and R.W. Newbury. 1987. The environmental assessment of hydroelectric impoundments and diversions in Canada. In: *Canadian Aquatic Resources. Can. Bull. Fish. Aquat. Sci.* 215. Pp 71-104.
- Rosenberg, D. M., R. A. Bodaly, and P. J. Usher. 1995. Environmental and social impacts of large scale hydroelectric development: Who is listening? *Global Environmental Change*. Vol 5. (2)127-148
- Ruth, M. 1994. A system dynamics approach to modeling fisheries management issues: Implications for spatial dynamics and resolution. *System Dynamics Review*, Vol. 11(3):233-243.
- Ruth, M. and J. Lindholm. 1996. Dynamic modeling of multi-species fisheries for consensus building and management. *Environmental Conservation* 23(4):332-342.
- Ryan, P. M. 1980. Fishes of the Lower Churchill River, Labrador. *Fish. Mar. Serv., Canada, Tech. Rep.* 922.
- Ryan, P. M., and J. J. Kerekes. 1988. Characteristics of sport fish populations in six experimentally fished salmonid lakes of Gros Morne National Park, Newfoundland. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1636.

- Ryder, R. A. 1977. Effects of ambient light variations on behaviour of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Bd. Can. 34:1481-1491.
- Sadar, H. M. 1994. Environmental Impact Assessment. Carleton University Press. Ottawa, Ontario. Canada.
- Sammons, S. M., C. G. Scalet and R. M. Neumann. 1994. Seasonal and size related changes in the diet of Northern Pike from a shallow prairie lake. J. Freshwater Ecol. (9) no. 4 321-329.
- Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm. 1(2):27-54.
- Schaefer, M. B. 1968. Methods of estimating effects of fishing on fish populations. Trans. Am. Fish. Soc. 97:231-241.
- Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Bd. Can. Bull. 184. 966p.
- Seaburg, K. G., and J. B. Moyle. 1964. Feeding Habits, digestion rates, and growth of some Minnesota warm-water fishes. Trans. Am. Fish. Soc. 93:269-285.
- Siegfried, C. A. 1987. Large-bodied crustacea and rainbow smelt in Lake George, New York: trophic interactions and phytoplankton community composition. Journal of Plankton Research. 9(1):27-39.
- Simonovic S. P. and D. H. Burn. 1989. An improved methodology for short-term operation of a single multipurpose reservoir. Water Resources Research. Vol. 25, No.1:1-8p.

- Simonovic, S. P., F. Hussam, and A. El-Shorbagy. 1996. The use of object-oriented modeling for water resources planning in Egypt. *Water Resources Management*, 11:243-261.
- Strange, N.E., R. J. P. Fudge and R.A. Bodaly. 1991. Post-impoundment response of a boreal northern pike (*Esox lucius*) population in Wupaw bay, Southern Indian Lake, Manitoba, 1976-88. *Can. Tech. Rep. Fish. Aquat. Sci.* 1823:v + 48 p.
- Svirskaya A. N. and M. N. Ivanova. 1990. Aspects of feeding and growth in juvenile Northern Pike, *Esox lucius*. *J. Ichthyol.* 30(1) 85-93.
- Swanson, G. M., K. R. Kansas and R. F. Remnant. 1988. A report on the fisheries resources of the lower Nelson River and the impacts of hydroelectric development, 1987 data. Manitoba Natural Resources Fisheries Branch. 297p.
- Swenson, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and Western Lake Superior. *J. Fish. Res. Bd. Can.* 34:1643-1654.
- Tautz, A., P. A. Larkin, and W. E. Ricker. 1969. Some effects of simulated long-term environmental fluctuations on maximum sustainable yield. *Journal of the Fisheries Research Board of Canada.* 26:2715-2726.
- Taylor, W. W., and M. H. Freeberg. 1984. Effect of food abundance on larval lake whitefish, *Coregonus clupeaformis*, growth and survival. *J. Fish. Biol.* 25:733-741.

- Terrell, J. W., T. E. McMahon, P. D. Inskip, R. F. Raleigh, and K. L. Williamson. 1982. Habitat suitability index models: Appendix A. Guidelines for riverine and lacustrine applications of fish HIS models with the Habitat Evaluation Procedures. U.S. Fish Wildl. Serv. FWS/OBS-82/10.A. 54p.
- Teska, J. D. and Behmer, D. J. 1981. Zooplankton preference of larval lake whitefish. Trans. Am. Fish. Soc. 110:459-461.
- Therien, N. 1981. Simulating the Environmental Impact of a Large Hydroelectric Project. The Society for Computer Simulation, La Jolla, California. Vol. 9. no. 2. 118p.
- Tyler, A. V. 1974. User's manual for pisces, a general fish population simulator and fisheries game program. Technical Report 22, St. Andrews Biological Station, St. Andrews, New Brunswick, Canada.
- Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board. Can. 24:2355-2453.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth. Human Biology. 10:181-213.
- Wain, D. B. 1993. The effects of introduced rainbow smelt *Osmerus mordax* on the indigenous pelagic community of an oligotrophic lake. Unpublished MSc thesis, University of Manitoba, Winnipeg, MB. 131 p.
- Wajdowicz, Z. 1964. The development of ichthyofauna in dam reservoirs with small variations in water level. Hydrobiol. 6(1):61-79.
- Walburg, C. H., G. L. Kaiser, and P. L. Hudson. 1971. Lewis and Clark Lake tail-water biota and some relations of the tail-water and reservoir fish populations. In: Hall, G. E. (ed.). Reservoir Fisheries and Limnology: 449-467.