

A Quantitative Life-Cycle Model to Identify Research Priorities and
Test Management Strategies for the Mackenzie River Broad
Whitefish (*Coregonus nasus* Pallus)

By

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**A QUANTITATIVE LIFE-CYCLE MODEL TO IDENTIFY RESEARCH PRIORITIES AND
TEST MANAGEMENT STRATEGIES FOR THE MACKENZIE RIVER BROAD
WHITEFISH (Coregonus nasus Pallus)**

**BY
TREVOR M. THERA**

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree
of
MASTER OF SCIENCE**

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ABSTRACT

Effective management of the Mackenzie River broad whitefish (*Coregonus nasus Pallus*) requires detailed knowledge of life history and an overall understanding of the dynamics of the system. I propose a simulation modeling framework for analyzing the life cycle of the broad whitefish and for identifying areas where future research should be conducted. The model incorporates all sources of mortality (density-dependent, density-independent and fishing mortality) a broad whitefish may encounter during its entire life cycle. Due to the lack of empirical data, model parameters were varied randomly around a mean parameter value, which is defined by a normal distribution. Estimated means were calculated by drawing on data that about broad whitefish biology or that described similar phenomenon in related species, and through experimentation with the model. Sensitivity analysis was carried out using a series of simulations involving model parameters set at values that were determined to be at the high and low biological ranges for that parameter. Of the fourteen parameters analyzed elasticities ranged from -0.02 to 11.5. Screening analysis indicated that the two parameters involved with juvenile density dependence (P7, P8) were orders of magnitude larger than the four other parameters (P1, P3, P5, P12) that exhibited large elasticities. A 2^4 experimental design was used to quantify the effects and interactive effects of these four elastic parameters had on the model. I used the model to identify key areas where future research will benefit the management of the Mackenzie River broad whitefish. Model output was validated against harvest surveys and a survey of experts regarding adult

population size. Results suggest that current levels of exploitation are not significant. Four key areas requiring research were identified in addition to the ongoing, long term work required to explore and describe the role density dependence plays in the juvenile stage of the life cycle. These four areas are: 1) the proportion of eggs that hatch on the spawning grounds and describe factors that affect egg hatch; 2) empirical measurements of fecundity should be obtained for fish at each of the spawning areas on a continuing basis; 3) the proportion of larvae that become trapped in the delta lakes and the level of mortality suffered by these fish, and 4) the ratio of fish being caught during their pre-spawning migration and during their downstream or post-spawning migration.

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CHAPTER ONE

INTRODUCTION

1.0 Background

Attempts to understand the ecology of fish resources, and the assessment of the abundance and biological state of fish resources have been a major endeavour of fishery scientists for approximately 100 years (Megrey and Wespestad 1989). The broad whitefish (*Coregonus nasus* (Pallas)), (Figure 1) of the Mackenzie Delta present a complex problem for fishery managers. The complexities involved in identifying individual stocks, estimating stock size, and determining the extent to which the population is exploited makes management extremely difficult.

Broad whitefish in the Mackenzie River exhibit a complex life cycle and a life history which reflects the physical complexity of the system they inhabit (Reist and Bond 1988, Fechem et al. 1992, 1995 a, b). During juvenile stages of the life cycle, broad whitefish occupy freshwater, estuarine and marine environments on an annual basis to feed and overwinter. After sexual maturity, broad whitefish migrate from freshwater systems on Richard's Island and the Tuktoyaktuk Peninsula (Kukjuktuk System, Canyonek System), (Lawrence et al. 1984) through the marine/estuarine corridor of the Beaufort Sea to the Mackenzie Delta. They continue to migrate up the Mackenzie River to their spawning grounds (Figure 2). Mature broad whitefish remain in the Mackenzie

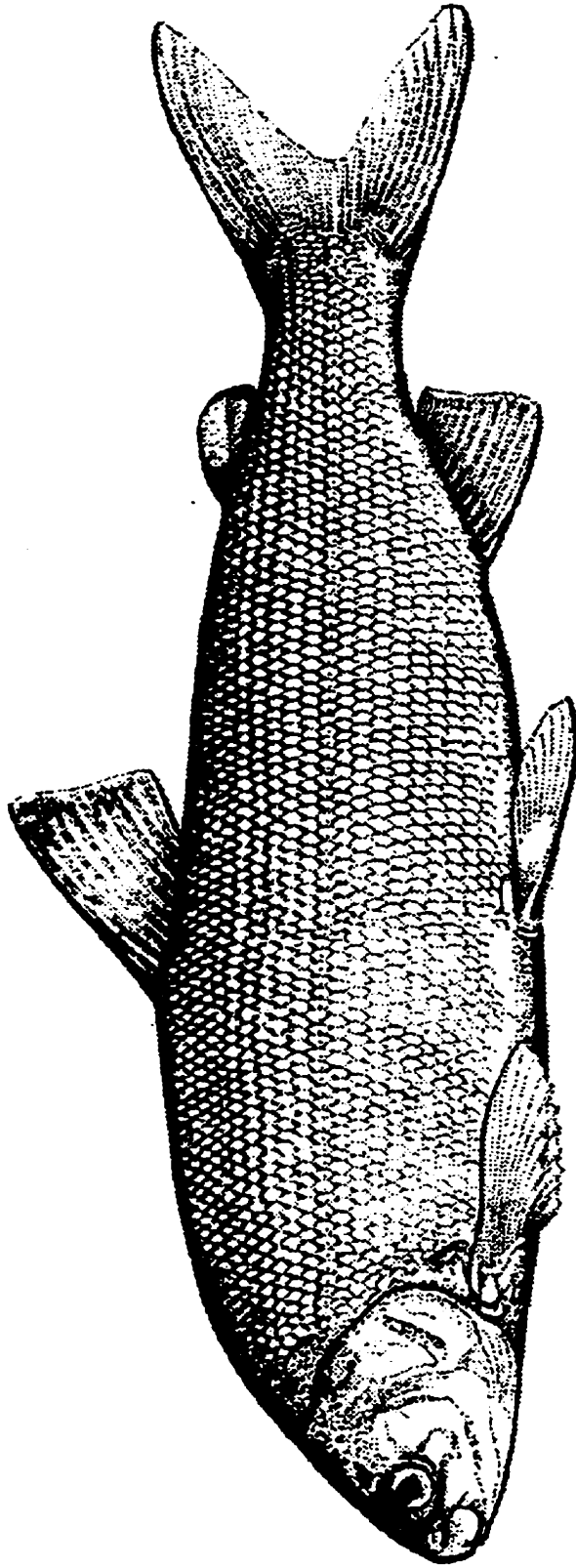


Figure 1. Adult broad whitefish (after Scott and Crossman 1973).

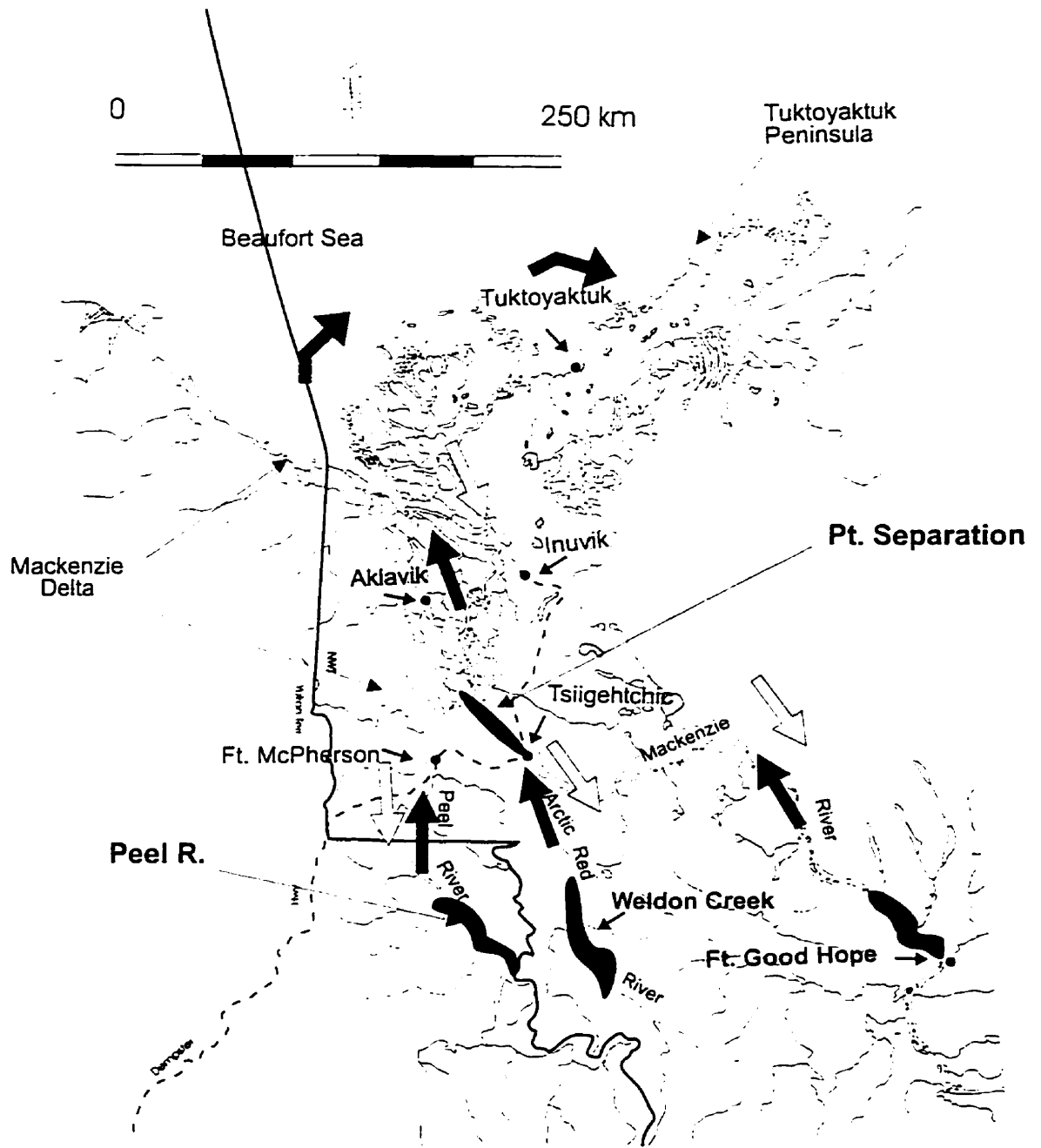


Figure 2. Suspected spawning locations (shown in black - Pt. Separation, Peel River, Weldon Creek, and Fort Good Hope) of the Mackenzie River broad whitefish according to Chang-Kue and Jessop (1992). Grey shaded arrows indicate downstream migration of larvae to the freshwater lake systems on the Tuktoyaktuk Peninsula. Black Arrows illustrate downstream migration of larvae from spawning grounds to rearing grounds.

River system either feeding in the estuarine regions of the delta or migrating to distant regions in the mainstem of the Mackenzie or its tributaries.

There have been several unsuccessful attempts to develop an export commercial fishery for broad whitefish in the Mackenzie Delta (Treble and Read 1994, Treble 1996). Despite this experience, recent recipients of land claim settlements (Inuvialuit and Gwich'in), (see below), have expressed interest in the development of a commercial fishery for broad whitefish in the future. However, such development must be accomplished in the presence of a large subsistence fishery.

Currently, the large subsistence fishery impacts this resource at a level many orders of magnitude greater than any previous commercial endeavor (Treble 1996). Many people from the Mackenzie Delta area fish for broad whitefish to feed their family and friends. Fishing for broad whitefish is also a cultural activity, and a way of life that is highly valued (Treble 1996). The subsistence fishery for broad whitefish is still of strong social and cultural importance and a core group of fishermen in each community rely on this fishery for their livelihood (Treble 1996).

The migratory nature of this species and the geographically complex nature of this system present a difficult management situation to fisheries managers. Broad whitefish regularly cross boundaries between the land claim areas of the Inuvialuit (Mackenzie Delta Inuit), Gwich' in (Dene Indian) and Sahtu (Dene Indian) peoples, (Figure 3) (Treble 1996). The migratory behaviour of the stock and the geographic location of fishing results in an

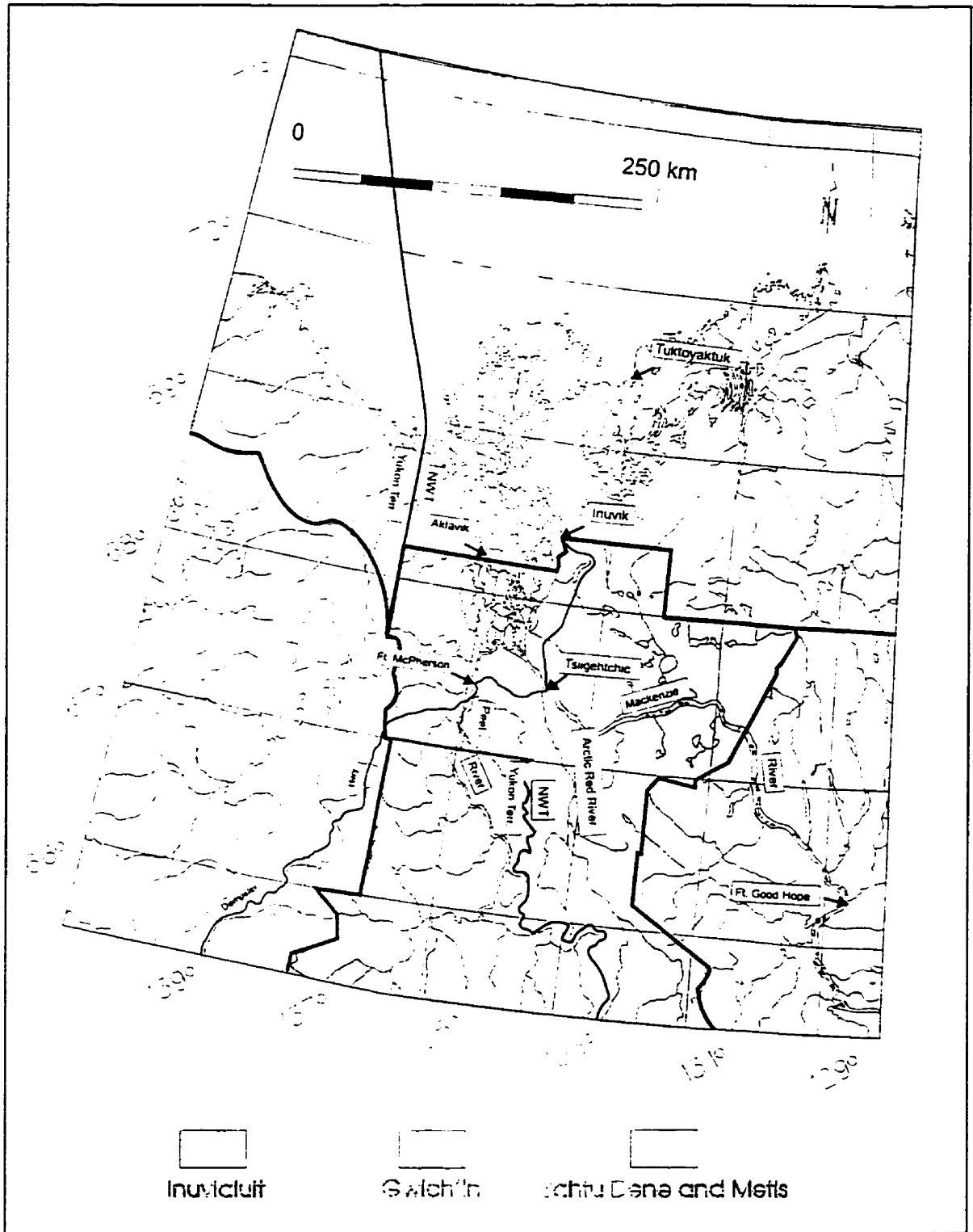


Figure 3. Comprehensive land claim regions covering the Lower Mackenzie River region. From Treble (1996).

"interception fishery" where fish are exploited in transit to, or from, their spawning grounds. This type of fishery is more difficult to manage than a "terminal fishery" where fish are exploited at or very near the spawning grounds. An interception fishery is more difficult to manage because Catch-Per-Unit-Effort (CPUE) data are not as effective as when managing an interception fishery (Tallman and Reist 1997). In the Mackenzie Delta area fish migrate through a vast array of channels during their spawning run. Exploitation occurs in static locations chosen by their proximity to communities. CPUE information could be used effectively only if fish were migrating through the same areas year after year, thereby being subject to the same level of effort each year. However, since fish may migrate through areas of exploitation some years and avoid these areas other years CPUE information is not useable. In a terminal fishery situation (CPUE) data can be used effectively, making the monitoring and management of the fishery much easier (Tallman and Reist 1997). In this case fish would always pass through known areas thereby being exploited with a known level of effort year after year. Because the broad whitefish fishery is an interception fishery, other types of information regarding the entire life cycle of the organism must be collected before the fishery can be adequately managed.

Important portions of the life cycle are completed within the boundaries of different land claim areas. Thus, actions taken in one land claim area can affect the abundance of broad whitefish in other land claim areas. Therefore, a holistic approach, involving knowledge of the entire life cycle of the broad whitefish, is

necessary to successfully manage subsistence harvests and potential commercial harvests in a manner acceptable to all land claim groups involved.

The vast geographic area, inability to monitor fishing effort, the high cost of data collection and the inability to collect biological data on a regular and consistent basis make scientific management difficult. Also, the complexity of fishery systems can make it difficult to comprehend all the system components and potential interactions (Lackey 1975, Johnson 1995). Models can help sort through the complexity and provide a clearer view of the system and the management problem.

1.1 Models in Fisheries Management

The use of mathematical models in fisheries work was established in the 1950's with the work of Ricker (1954) and by Beverton and Holt (1957), and even at this late date fisheries scientists were among the first to use simulation models in an applied renewable natural resource field. A model in the context of fisheries management can be described several ways and can have many uses. A model can merely be an account of organized and documented thinking. A model can also be defined as a simplified representation of a process, for example growth, or a system, for example a population, fishery, or waterbody (Starfield and Bleloch 1986). A model should not be viewed as "the system in a black box" but merely as a simplified representation of the real system that omits the trivial features of the system and focuses on the crucial components of the system (Johnson 1995). A model is essentially a hypothesis that states which

components of a system are crucial and shows how those components may function and interact. Determining what components are crucial features or trivial details depends on the question being addressed (Johnson 1995). Therefore, the first step in using models in fisheries management is to define how the model should be used (Johnson 1995).

Models can be used to make quantitative predictions in complex systems, organize and communicate concepts to others, and learn about or explore the system in question. However, accurate quantitative predictions require massive amounts of data from the system or species in question. This is the most dangerous use of models and also the most rare. Expectations of these types of modeling approaches are often unrealistic and can limit a model's usefulness (Hurley 1986, DeAngelis 1988). Models are most useful when applied as tools to help organize and communicate ideas to others. They also help managers learn more about the system in question and potential management options, and help focus attention on assumptions, critical factors, and the system's boundaries rather than being applied as strictly quantitative predictors (Johnson 1995).

1.2 Model Selection

Computer models can be powerful tools for addressing many of the problems that frequently occur in fisheries management. A computer simulation model is an appropriate method to overcome some of these problems because it will help identify knowledge and data gaps and suggest priorities for basic research projects (Megrey and Wespestad 1989). A simulation model can be

customized to the unique problems and contingencies regarding the broad whitefish and their biology. It may allow us to determine what components of this population are the most important and how they interact to produce changes in abundance (Wright 1992). Such models can be used to focus and justify ongoing research and data collection or identify research opportunities that will have the greatest impact on fisheries management (Lackey 1974; McLoughlin 1993). A model can also be used to organize concepts, communicate complex systems to others, and focus discussions. A model that is well structured can ensure continuity of the management process (Johnson 1995). New personnel can quickly learn about the system and understand what major processes are integral components to the system's overall functioning.

1.3 Systems Analysis and Simulation Modeling

Systems analysis is both a philosophical approach and a collection of techniques (including simulation) developed explicitly to address complex problems (Grant 1989). Systems analysis emphasizes a holistic approach to problem solving involving the use of mathematical models to identify and simulate important characteristics of complex systems. It has been applied successfully in engineering, industrial production, business management, and economics. This approach is also finding increasing application in biology, ecology, and renewable resource management (Grant 1989).

The benefits of a systems approach in wildlife and fisheries work, such as the emphasis that it places on a clear delineation of program objectives and its

usefulness in identifying areas where critical data are lacking, are well accepted (Grant 1989). Simulation is one component of systems analysis; it is the process of using a model to mimic or trace in step-by-step fashion the behaviour of a system (Grant 1989). Simulation models may be used in research to test hypotheses about the system, or in management to forecast system behaviour (Machiels et al. 1994). In the case of the broad whitefish, the reductionist approach to elucidating the dynamics of the life cycle involves a large commitment of time and money without yielding sufficient insight into species dynamics within a reasonable time frame. Conversely, a systems modeling approach can help obtain answers to difficult questions that can be explored before being faced with managing this particular system. This gives the manager an immediate response or range of responses to the questions he or she may be faced with. This ability represents professional fisheries management at its best (Wright 1992). A simulation modeling approach also provides a framework for identifying and quantifying important factors in the life cycle of the broad whitefish. The great benefit of simulation is that it provides an experimental framework that can be used when experimentation with the corresponding real world system is either too costly or too difficult (Power and Power 1994). Also, real systems require the experimental treatments and run orders to be randomized. In simulation this is not necessary because there is complete control over all possible variables (Law and Kelton 1991). In addition to having complete control over the variables, simulation: 1) allows the experimenter to ask the "what if ?" question and explore a wide range of alternative approaches

to a problem; 2) it allows for detailed quantitative representations of interacting transient phenomena; 3) it provides the necessary time compression for studying the behaviour of alternative management schemes; and, 4) it identifies knowledge gaps and suggests priorities for research. Thus, I chose a systems analysis approach to represent and study all the interacting components of this fishery system.

Simulation is an efficient and powerful tool but it also has its inadequacies. These are as follows: 1) reasonable and realistic simulations are constrained by the lack of knowledge and empirical data describing the specific system, therefore the model may include many assumptions; 2) complex simulation models are difficult to communicate to others; 3) simulation models cannot be transferred to other systems; 4) since they are dependent on many variables, simulation models are subject to measurement error (Megrey and Wespestad 1989).

A simulation modeling approach involving sensitivity analysis is an excellent method to create a framework to organize the available information, test different hypotheses or approaches to management, help in research-planning and identify key items needing further study. Sensitivity analysis can be defined as the process of quantifying the amount of change in model output resulting from a known change in an input parameter. Constructing the simulation model allowed for the development of hypotheses describing the life cycle of the broad whitefish, which can be tested in time through focused

research. The simulation model also pointed out areas of our knowledge that were incomplete regarding the life cycle of the broad whitefish.

All effective simulation studies make use of an iterative and cyclic process. Each cycle consists of a stage of sample collection and a stage of modeling analysis. The following cycle of this loop should consider the information obtained in the previous stage. Therefore the next stage of empirical data collection can be done in a more focused manner (Lackey 1975, Sukhanov et al. 1990, Keen and Spain 1992) (Figure 4). An information model is a dynamic product of iterative feedback from the analysis process (Kerr and Neal 1976). The use of an information model in conjunction with computer simulation techniques is an effective method of exploring complex problems.

Computer simulation is increasingly used as a basic tool for the analysis of fishery systems. There are several examples of successful simulation studies in the literature. Larkin and Hourston (1964) and Larkin and McDonald (1968) used computer simulation models to study the combined interrelations of a large number of variables in order to generate new biological hypotheses and to narrow the areas of ignorance concerning population phenomena. This model also serves as a dynamic archive of the existing knowledge of the Skeena River sockeye. Simulation results suggested that there was a lack of understanding of mechanisms determining age of return and the existence of density dependant mortality (Larkin and McDonald 1968). Johnson et al. (1992) and Millman et al. (1992) used a simulation model as a learning tool. They combined the

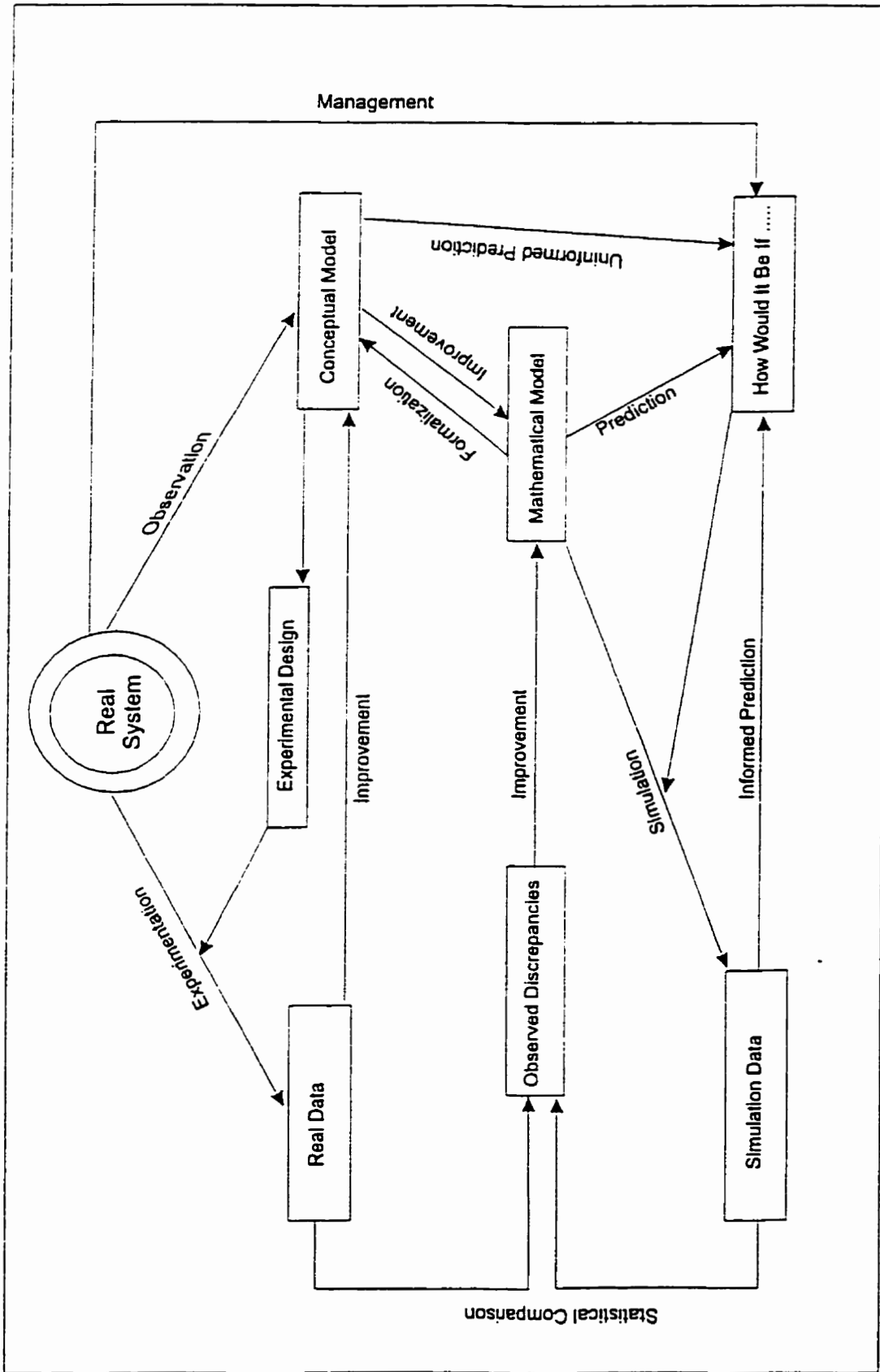


Figure 4. A diagram showing the role of quantitative modeling and simulation within the process of research. Based on part on a diagram by Gerardin (1968). After Keen and Spain (1992).

modeling techniques of sensitivity analysis and policy comparisons to develop conclusions that were appropriate under a variety of uncertainties (Johnson 1995).

Marttunen (1992) used a simulation model to study the effects of lake regulation on European whitefish stocks. The main focus of the model was on the changes in reproduction and food resources, and the subsequent effects on fish stocks and catches. Overholtz and Tyler (1986) and Kruse and Tyler (1989) used a simulation model in an exploratory framework. Rather than trying to create predictive models of the George's Bank fish community and of the recruitment mechanisms of the English Sole off the coast of Oregon they devised simulation models to pose and test hypotheses about the ecological mechanisms that may be at work in these systems. Morin and Doidge (1992), developed a matrix population model for anadromous coregonids which helped investigate the population dynamics and complex life cycles of cisco (*Coregonus artedii*) and lake whitefish (*Coregonus clupeaformis*). This model focused research on important transitions between life stages and provided a general context for improving the understanding of coregonid demography.

All of the models proved to be a useful means of organizing ideas and information. Some hypotheses were supported and an overall understanding of the systems were gained. Data requirements necessary for the management of the fisheries were also highlighted.

In this study a quantitative theoretical model describing the life history components for the Mackenzie River broad whitefish is constructed. A systems

analysis approach is used to combine and organize most of the available information regarding the Mackenzie River broad whitefish. Creating a quantitative framework, which describes the major components of the life cycle of the Mackenzie River broad whitefish may ultimately allow for the testing of hypotheses describing the system or predicting the behaviour of the system. As more focused empirical data are collected throughout successive cycles of the research loop described above, our understanding of how the system works will increase over time, allowing the predictive ability of the model to increase as well. However, the main objective herein is to identify, rank, and explain the key components of the life cycle of the broad whitefish and their interactions with the fishery. To accomplish this I built and validated a model that takes into account what is currently known about the life-cycle of the Mackenzie River broad whitefish stocks. Then, I used the model in sensitivity tests to rank the assumptions and parameters in terms of their effect on the output of the model. I further examined four out of the six most important parameters in the model in an experimental design framework in order to quantify their importance and determine important interactive effects between parameters. Important interactions between parameters noted as having considerable effect on model output are ranked according to their importance to the simulated system. I used this information to suggest where future research activities should be placed. Finally, I used the model to explore issues pertaining to the exploitation of these stocks. This information may help clarify or dismiss current assumptions regarding the exploitation of this population.

CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

The future challenge in improving the assessment of populations and biologically based harvest policies is to improve our understanding of the dynamics of life processes in fish populations and their response to density - dependent and density-independent factors (Megrey and Wespestad 1989). The current state of our knowledge regarding the geographical area of the study, the basic biology and life cycle of the broad whitefish, the fishery and processes that regulate the abundance of the population is described below from a comprehensive survey of the literature. Detailed knowledge about the biology and life cycle of the Mackenzie River broad whitefish is largely obtained from recent studies beginning with Jessop et al. (1974), Bond and Erickson (1982, 1985, 1987), and Chang-Kue and Jessop (1993). Many questions regarding the biology and life cycle remain unanswered. In this study, gaps in knowledge regarding the broad whitefish are dealt with by using analogues from other closely related species such as lake whitefish (*Coregonus clupeaformis* Mitchell) that help to parameterize the model. When this information was unavailable assumptions were made based on expert opinion.

Hypotheses regarding the dynamics of this population are tested. Processes that regulate the abundance of the broad whitefish population are proposed and tested in the simulation model. Density-dependent and density-independent processes that operate in similar systems are assumed to operate in the Mackenzie River system and are described in section 2.5.

2.2 Description of the Natural System

The Mackenzie River is the fourth largest river flowing in the Arctic and the largest in North America (Greene 1978). The Mackenzie River Basin occupies a

total area of 1.8×10^6 km², including seven major tributary rivers, three major lakes and three major deltas, and a drainage basin that possesses a diverse array of aquatic habitats (Baker and Reist 1988, Reist and Bond 1988, Bond and Erickson 1992). Northern reaches are ice-covered from September to late June, while southern areas are ice-covered from mid-November to late April. The Mackenzie River flows all year round with peak flow rates of 2.3×10^3 m³ sec⁻¹ during June break-up (Bodaly et al. 1989). Major tributaries that are of importance in this study are the Peel River and the Arctic Red River. These tributaries contain important spawning grounds for the broad whitefish (Reist and Bond 1988, Bodaly et al. 1989, Bond and Erickson 1992, Tallman and Reist 1997). As the Mackenzie River plume enters the Beaufort Sea, generalized storm tracks from the west and the Coriolis effect deflect it toward the northeast, across the outer delta and along the coast of the Tuktoyaktuk Peninsula (Reist and Bond 1988) (Figure 2). This provides a large area of freshened water extending across the outer delta and east along the Tuktoyaktuk Peninsula, which is used as a migratory corridor by broad whitefish of all life history stages. The nearshore area west of the Mackenzie River Delta is much different. During winter, the smaller rivers freeze to the bottom and the coastal zone becomes highly saline. This differential distribution of freshwater is thought to be an important determinant of the distribution and movements of anadromous fishes in coastal habitats of the southern Beaufort Sea (Reist and Bond 1988).

The Tuktoyaktuk Peninsula, Richard's Island and some areas of the outer delta contain freshwater lakes that are important rearing grounds for juvenile broad whitefish (Lawrence et al. 1984, Bond and Erickson 1985, 1992, Bodaly et al. 1989, Chang-Kue and Jessop 1992). Juveniles enter the lakes through freshwater creeks along the coast (e.g. Kukjuktuk Creek, Canyonek Creek, Freshwater Creek) (Chang-Kue and Jessop 1992) (Figure 5). These tundra

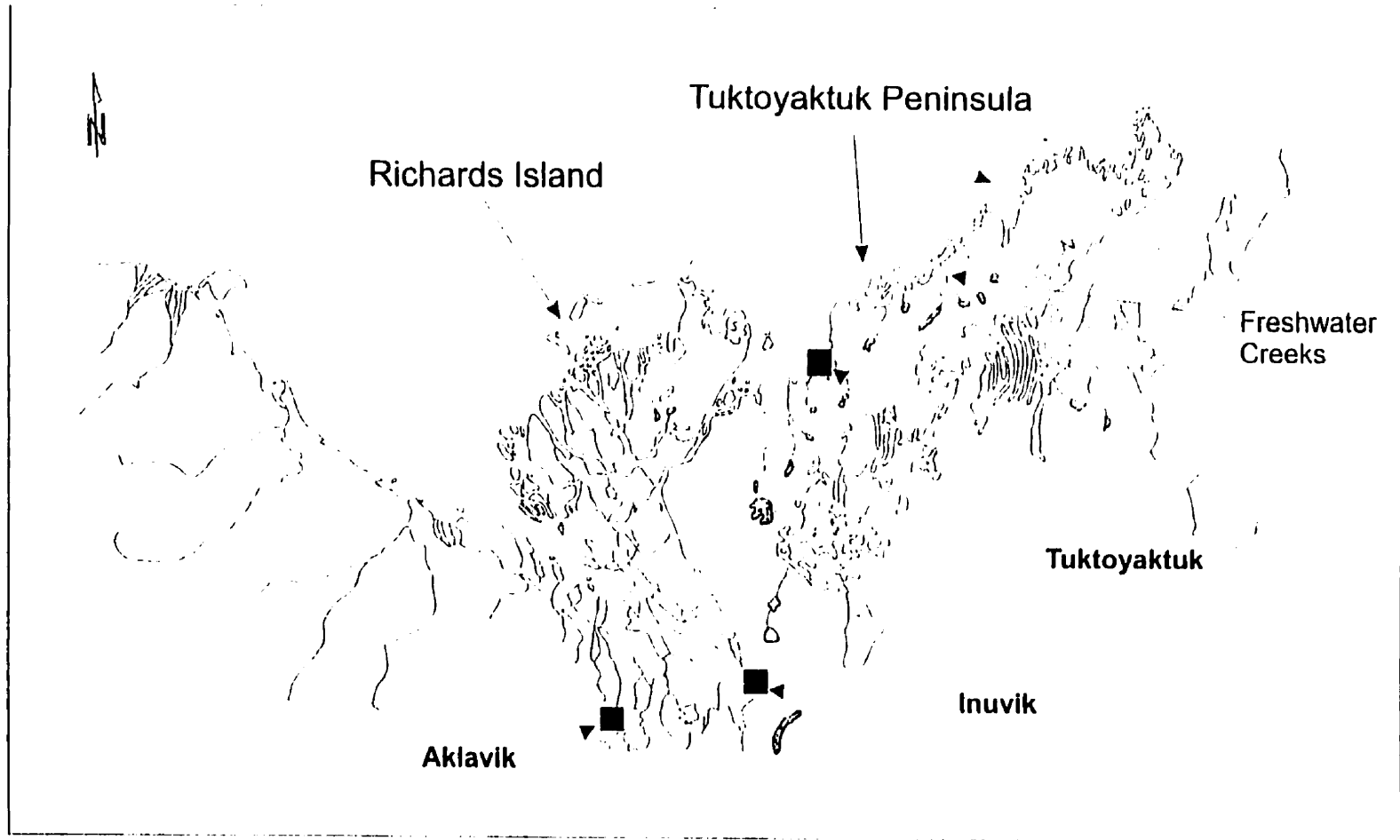


Figure 5. The outer Mackenzie Delta highlighting major rearing grounds for juvenile broad whitefish. Rearing grounds are located in freshwater lake systems on Richards Island and on the Tuktoyaktuk Peninsula indicated by arrows. The settlements of Tuktoyaktuk, Aklavik, and Inuvik are shown by grey shaded squares.

lakes are generally clear of ice by 30 June (Burns 1973). The average area of the lakes ranged between 87 to 1854 hectares on the Tuktoyaktuk Peninsula and from 11 to 523 hectares on Richard's Island. The maximum depths ranged from 1.0 - 9.5 m (Lawrence et al. 1984). The lakes have warm summer water temperatures (up to 18.5 °C) and abundant populations of benthos and plankton. These conditions may provide nearly ideal growing conditions in a region where the growing season is restricted (Bond and Erickson 1985).

Broad whitefish stocks are fished between Fort Good Hope and the Weldon Creek area in the south and the southern Beaufort Sea and Tuktoyaktuk Peninsula in the north encompassing 66°N to 70°N Latitude, (Figure 6). The four shaded areas on Figure 2 show the suspected spawning locations of the broad whitefish. During the spawning migrations fish are exploited at various locations. Major areas of exploitation are: Shingle Point, Whitefish Station, the Horseshoe Bend area and the communities of Tuktoyaktuk, Aklavik, Fort McPherson, Tsiigehtchic and Fort Good Hope (Figure 6).

2.3 Biology of the Broad Whitefish

The Mackenzie River broad whitefish has received considerable attention since the increase in hydrocarbon exploration in this area beginning in the late 1970's. Hatfield et al. (1972a, 1972b), Stein et al. (1973a, 1973b), Jessop et al. (1974), Jessop and Lilley (1975), Percy (1975), Taylor et al. (1982), Chang-Kue and Jessop (1983), Lawrence et al. (1984), Bond and Erickson (1985), and Strange (1985) provided information for basic biological questions about the broad whitefish. Recent land claim settlements in the area and the importance of the broad whitefish in the native subsistence fisheries allowed local management boards and the Department of Fisheries and Oceans to launch a variety of monitoring programs, such as the Inuvialuit Harvest Study, the

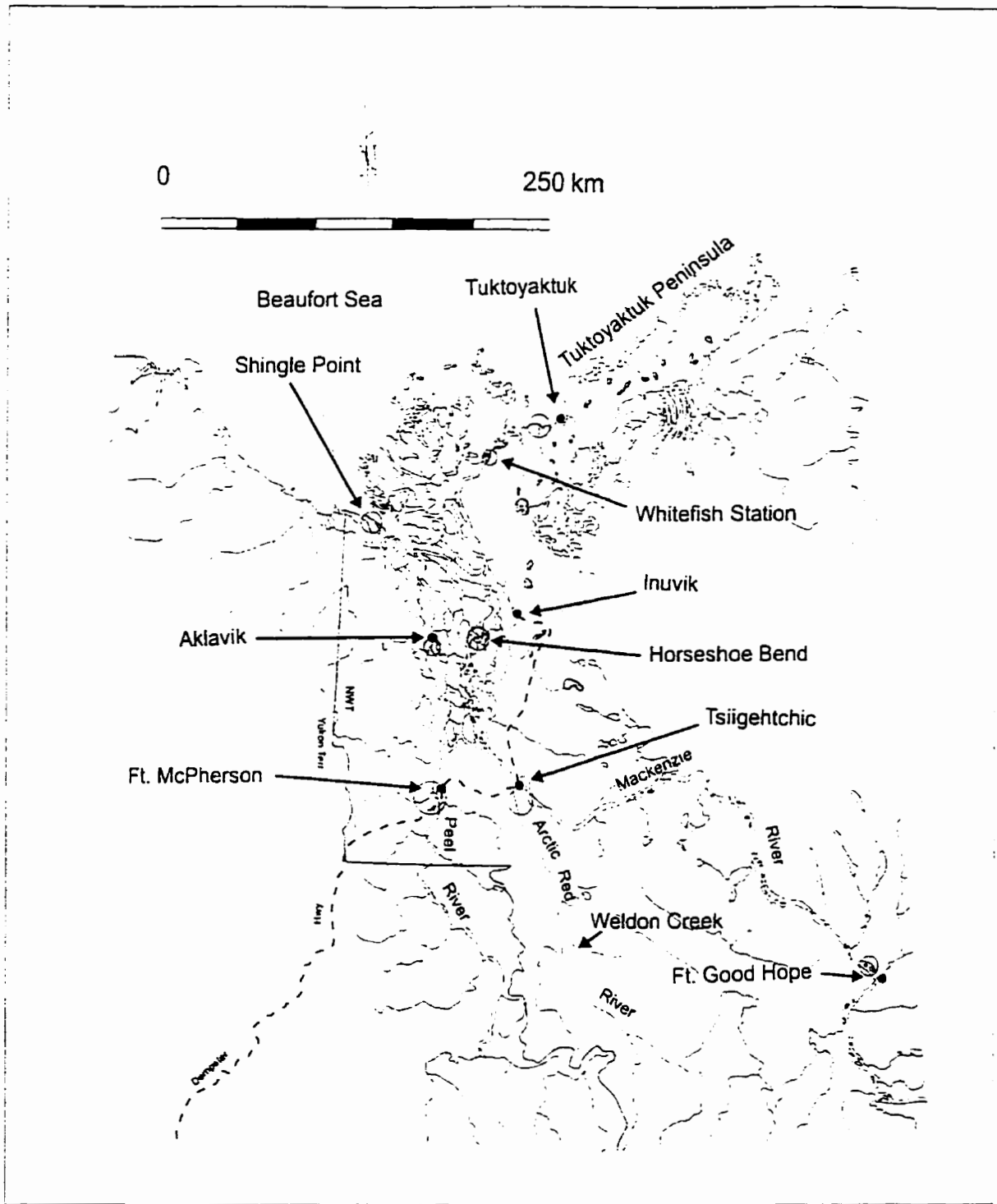


Figure 6. Communities and important areas in the lower Mackenzie River and Delta. Grey shaded circles indicate major areas of exploitation. Communities are shown by small black circles.

Gwich'in Harvest Study and several programs carried out by the Department of Fisheries and Oceans (de March 1989, Chang-Kue and Jessop 1992, 1993, 1997 a, b, c, and Tallman and Reist 1997).

Broad whitefish possess a complex life cycle and life-history and are thought to exhibit some degree of anadromy. Fechelm et al. (1995 a and b), described them as amphidromous fish which have evolved a complex life history and life cycle that reflects the complexity of the system they inhabit. McCart (1985) categorized broad whitefish as a type III anadromous fish; because after a seaward migration, they occupy estuarine and marine environments for only a short period before again entering fresh water to feed.

Fish larger than 27 mm were observed to tolerate salinities 20‰ or greater (de March 1989). However, the preferred salinities appear to be 20 ‰ or less (deMarch 1989). Thus, broad whitefish appear to use coastal, saline habitats primarily as migration pathways between separate spawning, overwintering, and feeding areas in freshwater.

Broad whitefish larvae are flushed northward from the spawning areas in the upper reaches of the Mackenzie, Peel, and Arctic Red Rivers by the spring freshet (Reist and Bond 1988). Larvae generally travel eastward along the still ice-covered coasts of Richard's Island and the Tuktoyaktuk Peninsula aided by the Coriolis Effect on the plume of freshwater from the Mackenzie. Upon reaching the mouths of one of the many small freshwater systems on Richard's Island or the Tuktoyaktuk Peninsula (e.g. Kukjuktuk System, Canyonek System, Freshwater System, Mayogiak System), the larvae migrate upstream and remain in these systems for the first several years of their life (Bond and Erickson 1985, Chang-Kue and Jessop 1992), (Figure 5). Walters and Ludwig (1981) and Fischer and Pearcy (1984) indicate that the critical elements during the first year of a fish's life are interrelationships among dispersal, feeding success, growth

and predation. Broad whitefish likely benefit from a rapid and early growth rate due to an abundant food supply, and a reduced level of predation in the tundra lakes of the outer Delta and Tuktoyaktuk Peninsula (Strange 1985). The larval stage is a period when a fish is potentially very susceptible to predation, so larvae which can rapidly grow to a less vulnerable size have a survival advantage (Taylor and Freeberg 1984, Rice et al. 1987, Viljanen 1988, Freeberg et al. 1990, Salojarvi 1992 a and b, Lehtonen et al. 1995). Therefore, by avoiding these critical elements during the first year of life, broad whitefish increase their chance of surviving to sexual maturity. Faster growth also means the fish may join the spawning stock at a younger age (Bond and Erickson 1985). Most of the fish that remain in the lakes are young-of-the-year and yearlings that remain there to grow and mature for several years (approximately 6 - 8). After reaching maturity fish migrate along the coast to the delta area where they join the existing adult component of the population. This adult component of the population migrates upstream and spawns in the Mackenzie, Peel, or Arctic Red Rivers (Lawrence et al. 1984, Bond and Erickson 1985, Chang-Kue and Jessop 1992).

The mean length of adult Mackenzie River Broad whitefish ranges from 450 - 474 mm and the average weight is two kilograms or greater (Bond and Erickson 1985, Taylor et al. 1982, Chang-Kue and Jessop 1992). The mean age for the Mackenzie River broad whitefish population is 12 years, but fish as old as 30 years are regularly caught (Treble and Tallman 1997). The Mackenzie River broad whitefish population has a sex ratio of approximately 1:1 (Treble 1996). The value for mean fecundity is estimated to be approximately 44, 257 eggs per female with a standard deviation of (14 840) (Chudobiak 1996). This value is consistent with fecundity estimates ranging from (26, 922 - 65, 798) with a mean value of 39, 721 eggs per female (deGraaf and Machniak 1977). In order for managers to successfully manage this fishery all relevant aspects of the biology

including their life cycle, migratory patterns, inter - and intra - specific interactions of the broad whitefish must be fully understood.

2.3.1 Life Cycle of the Broad Whitefish

The life cycle of the broad whitefish is complicated. Managers must have a good understanding of the life cycle in order to be successful (Reist and Bond 1988). The broad whitefish is thought to spawn once every two to three years. This multi-year cycle of reproduction is a common occurrence for most northern fish, especially the female sex (Roff 1992). The short growing season, or dramatic climatic variation, may prevent fish from producing eggs. Therefore, individual northern fish often skip one or two years between successive spawning events to accumulate enough energy to spawn (Reist and Chang-Kue 1996). Thus during any given reproductive period, the population is divided into two segments, a non - spawning segment consisting of individuals which are developing or maturing for the first time and individuals that are sexually mature which will spawn that year. In July or August sexually mature, reproductive individuals begin migrations upstream to holding areas in the central delta. In September or October broad whitefish migrate further upstream to spawning sites where eggs are assumed to be broadcast onto a gravel substrate much like the reproductive behaviour of lake whitefish (Freeberg et al. 1990). A full description of the life cycle beginning with the hatching of the eggs on the spawning grounds follows.

2.3.1.1 Reproduction and young-of-the-year

There are four distinct spawning areas known to date (Figure 2). These are: 1) the Weldon Creek area on the Arctic Red River, which is approximately 160 kilometers upstream from the confluence of the Arctic Red River and the mainstem Mackenzie; 2) the area of Point Separation on the mainstem of the

Mackenzie; 3) the upper reaches of the Peel River and, 4) the area upstream of the Ramparts Rapids area on the Mackenzie River near the town of Fort Good Hope. The locations of these spawning areas have been determined from radio-tracking data (Chang-Kue and Jessop 1997 a). The latter site is the most distant of all of the spawning grounds, some 500 river km from the outer delta.

Maximum migration upstream on the Mackenzie River is to the Ramparts Rapids, which act as a natural barrier to broad whitefish movement further upstream on the Mackenzie River (Chang-Kue and Jessop 1993, 1997 a, b, c).

Broad whitefish spawn under the ice during late October and early November when the water temperature is approximately zero degrees Celsius (Chang-Kue and Jessop 1992). The fertilized eggs undergo development during the winter and hatch in late spring, which in this area is sometime during May. The date and the intensity of hatching is governed by the flow rate of the rivers (Bogdanov et al. 1991). This occurs because the broad whitefish embryo is sensitive to mechanical perturbations. It is thought that because broad whitefish larvae are well developed near the period of breakup the high flow rates may cause physical stimulation of the embryo to initiate hatching (Bogdanov et al. 1991). Because the four stocks are widely distributed geographically throughout the delta, it can be assumed that the dates of peak hatching periods can be obtained by determining the dates breakup occurs at each of the spawning grounds. For example, breakup occurs on or about May 20 in the Fort Good Hope area, while areas in the Arctic Red River and Peel River breakup on or about May 31 and Point Separation breaks up approximately a week later (Government of Canada - Water Directorate 1979 - 1990). Therefore, more southerly spawning grounds such as Fort Good Hope produce larvae sooner than the spawning grounds further north such as Point Separation. The larval

fish from all areas are flushed downstream under the ice during May and June to the delta and nearshore areas.

Broad whitefish young-of-the-year undergo one of three possible fates upon entering the Mackenzie Delta (Baker and Reist 1988, Reist and Bond 1988). 1) A small proportion (<10% of the larvae are carried westward along the Yukon north slope as far as Phillips Bay (Bond and Erickson 1987), (See Figure 2): 2) An unknown proportion may be swept into delta lakes by the high spring waters and may become isolated in these lakes once the water recedes (Baker and Reist 1988, Reist and Bond 1988). Individuals from this group which survive the winter in these lakes will be able to re-join the larvae in the Mackenzie River during the next flood as fish of the 1+ age category (Taylor et al. 1982). Older juveniles which may have spent more than one winter in these lakes may also leave these lakes during spring flood events. 3) The majority of the larvae are likely carried out through the delta from the spawning grounds to the coast where they will continue to be swept eastward along Richards Island and the Tuktoyaktuk Peninsula by the fresh water plume of the Mackenzie and the prevailing currents of the Beaufort Sea. Young-of-the-year and juveniles reach the coast in late May or June (Hatfield et al. 1972 a, b, Taylor et al. 1982, Bond and Erickson 1985, Chang-Kue and Jessop 1992). After reaching the coast they proceed along Richard's Island and the Tuktoyaktuk Peninsula, finding their way into freshwater streams and eventually into many of the productive freshwater lakes (Bond and Erickson 1985, Baker and Reist 1988, Reist and Bond 1988, Chang-Kue and Jessop 1992).

In the Kukjuktuk Creek drainage on the Tuktoyaktuk Peninsula the upstream migrations of juveniles to freshwater lakes contained a high proportion of young-of-the-year fish or 1 + fish. Eighty-eight percent of the broad whitefish upstream run in 1979 were 0 + and 1 + year old fish with modal fork lengths of

(51 to 75 mm) (Figure 7) (Chang-Kue and Jessop 1992). Similarly, the majority of upstream migrants in the Freshwater Creek System were observed to be juvenile broad whitefish between the ages of 0+ and 1+ years (Bond and Erickson 1985). Juveniles caught in estuarine areas such as Kugmallit Bay with seine nets ranged from 49 - 64 mm, and fork lengths less than 75 mm were reported for 0+ aged fish in creeks on the Tuktoyaktuk Peninsula (Bond and Erickson 1985).

A large number of fish entering the estuarine areas are assumed to be unsuccessful in reaching the lakes during their first year due to intolerable saline conditions in the estuary later in the summer. Reist and Bond (1988) proposed that these fish spend their first winter within delta or coastal habitats that are freshened by the winter flow from the Mackenzie River. They migrate into the freshwater streams on Richard's Island and the Tuktoyaktuk Peninsula the following spring as age 1+ fish (Reist and Bond 1988).

2.3.1.2 Juveniles

Immature broad whitefish remain in the tundra lakes up to four years before switching to complex annual migrations between lakes and coastal waters. (Bond and Erickson 1985, Chang-Kue and Jessop 1992). While in the lakes their diet changes from planktonic to epibenthic food and their average fork length increases to more than 250 mm. Then during years four through eight they make brief spring migrations out of the lakes to the coast to make use of the productive estuarine habitat for feeding (Bond and Erickson 1985, Chang-Kue and Jessop 1992). At the end of summer they return to the lakes to overwinter (Chang-Kue and Jessop 1992). They remain in these lake systems until the onset of sexual maturity at approximately seven or eight years of age

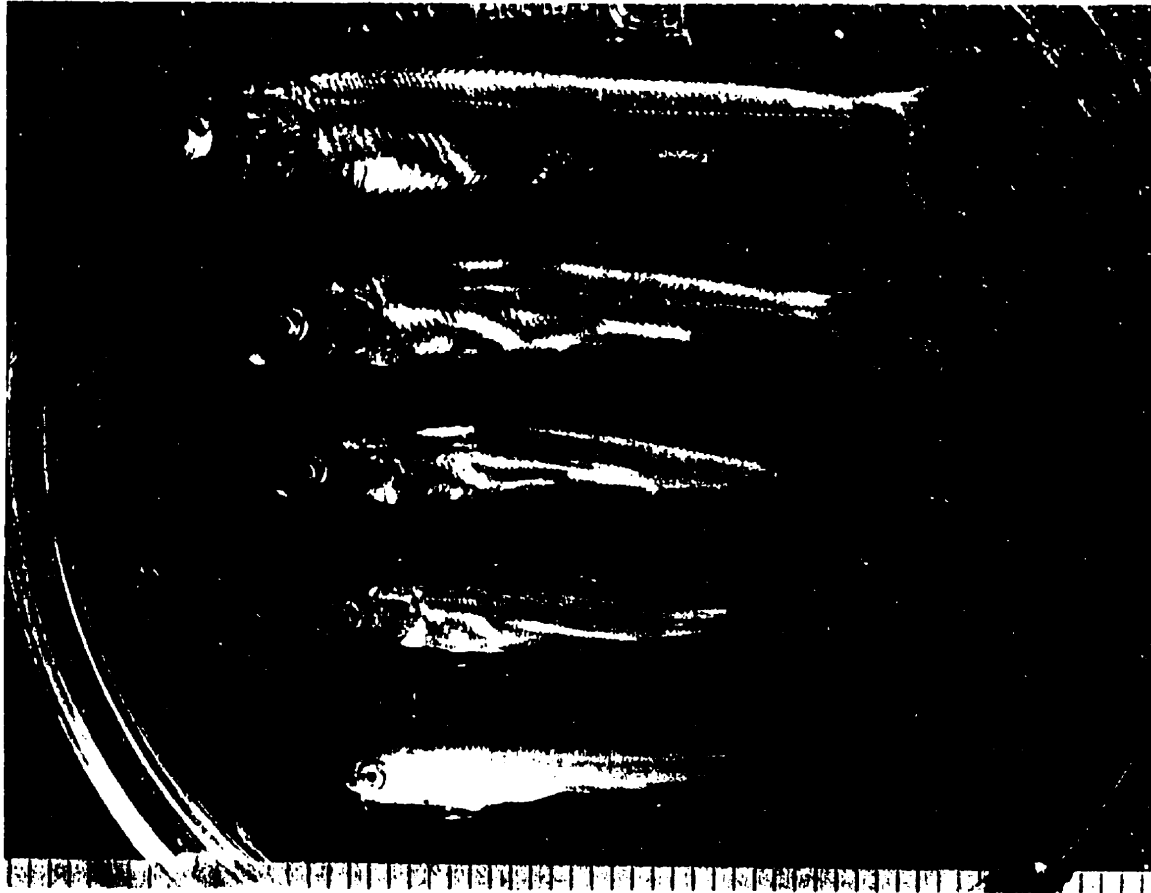


Figure 7. Size ranges of lower Mackenzie River juvenile broad whitefish. Photo illustrates the wide variety of size ranges found in the tundra lakes. Photo taken by Ken Chang-Kue near Kujuktuk Creek, Northwest Territories.

(Bond 1982, Bond and Erickson 1985, 1987, Reist and Bond 1988, Baker and Reist 1988, Chang-Kue and Jessop 1992).

Individuals which are sexually maturing for the first time, move out of the lakes in July and enter the delta, mixing with the adult component of the population (Bond and Erickson 1985, Chang-Kue and Jessop 1992). These fish may now be recruited to the fishery. After leaving the shelter of the lakes and embarking on their long migrations they are subjected to a multitude of fishing pressures. As they travel westward along the coast of the Tuktoyaktuk Peninsula and enter the delta via the east channel of the Mackenzie they pass through two areas of intense exploitation. At Tuktoyaktuk harbour the fish are exploited by subsistence fishermen. Further westward, they are fished at Whitefish Station (Figure 6). The estimated number of broad whitefish harvested in each of these areas on an annual basis is near 15, 000 (Treble 1996). The remaining first-time-maturing individuals that pass successfully through these areas of exploitation continue their migration southward where they become a component of the adult population.

2.3.1.3 Adults

The mature component of the population is divided into two segments; an adult spawning component and a developing or maturing component of first time spawners (Reist and Bond 1988). First-time-spawning-individuals reach the inner delta near mid-August to join the majority of the mature population at pre-spawning holding areas (e.g., Horseshoe Bend) (Figures 2 and 8), which are present in mainly deep eddies of major channels (Stein et al. 1973 a, b, Chang-Kue and Jessop 1992). Pre-spawning behaviour begins in mid to late August (Stein et al. 1973 a, b, Chang-Kue and Jessop 1983). Pre-spawning aggregation sites may also contain a considerable proportion of individuals from the developing component of the population (J. Reist and K. Chang-Kue personal

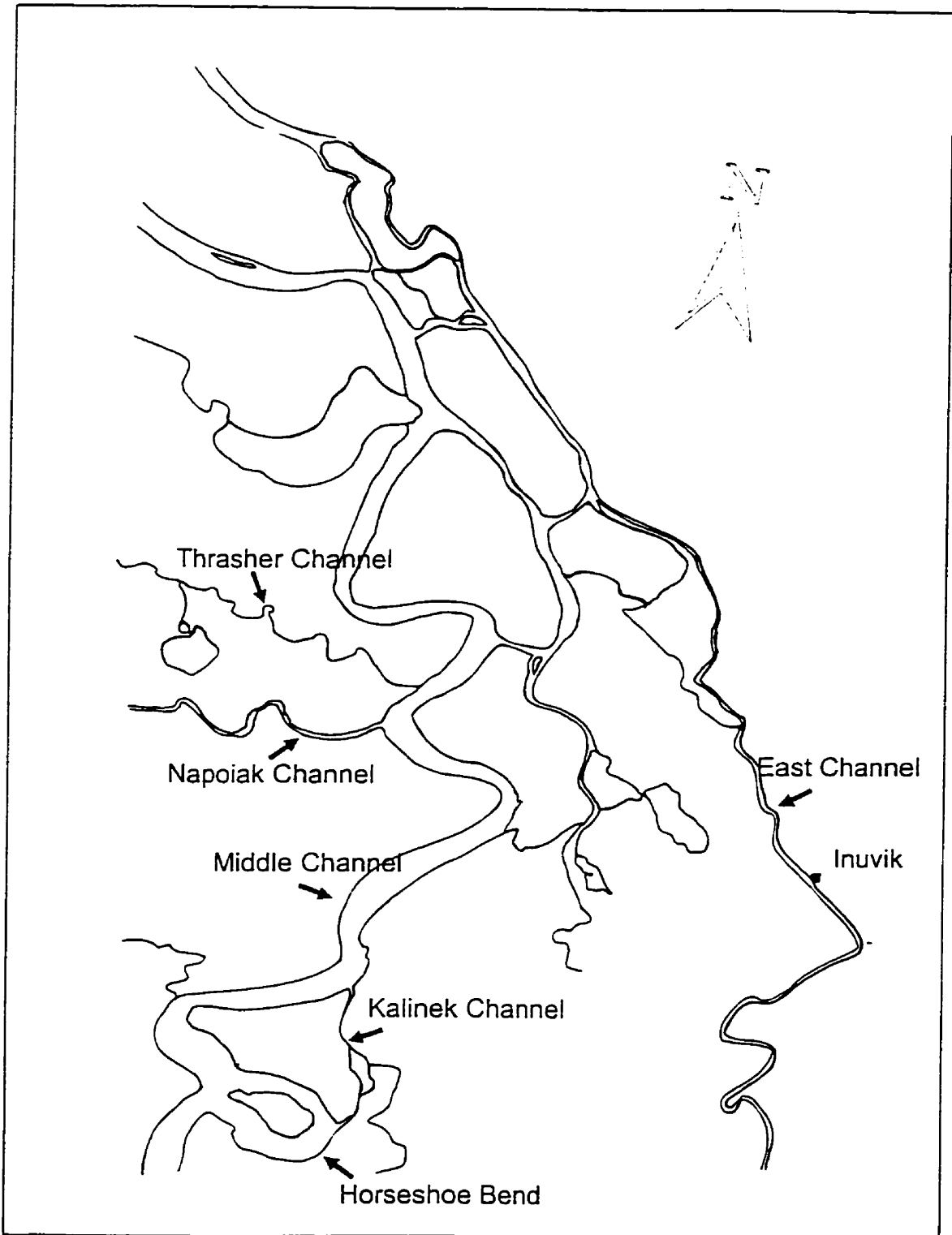


Figure 8. Locations of fish camps near the Horseshoe Bend area of the Mackenzie Delta comprising the 1989 - 1994 exploratory fishery (after Treble 1996a).

communication). Spawning individuals and developing individuals remain in this general area from late August to early October (Baker and Reist 1988). Exploitation by commercial and subsistence fishermen is intense in these areas (Treble 1996). Usually, fish are not concentrated in any one area for an extended period of time, due to their migratory behaviour. However, during the pre-spawning aggregation phase, large numbers of fish occupy a small area. This results in these fish being highly vulnerable to the amount of fishing effort (Hilborn 1979).

Thus, pre-spawning aggregation behaviour may increase the catchability represented by the coefficient "q" in the equation. Given that $F = Eq$.

$$q = F/E \quad (1)$$

Where: F = instantaneous fishing mortality,

E = fishing effort, and

q = catchability coefficient.

A higher "q" will mean a higher CPUE. Pre-spawning aggregations and the migrations of large numbers of individuals into narrow corridors will also cause "q" to increase due to a "bottle neck" effect (Hilborn and Walters 1992). Both of these behaviours increase the susceptibility of the fish to the gear, or will increase the catchability coefficient "q" in equation (1). Catch-Per-Unit-Effort calculations will be biased upwards and in turn estimates of the stock size will also be biased upwards. Other variables such as the variability in migratory routes or timing available to the broad whitefish may bias the CPUE downwards. Local subsistence and commercial fishermen use their knowledge of fish behaviour to maximize CPUE. Consequently, fishing pressure is great in these areas.

In early October the spawning segment of the population migrates upstream to their spawning grounds. However, it is suspected that the spawners

may be accompanied by significant numbers of the developing or resting segment of the population (J. Reist and K. Chang-Kue personal communication).

Reist and Bond (1988) and Chang-Kue and Jessop (1992) believe spawners move quickly upstream and presumably migrate to the general area where they were hatched. However, the degree and intensity of homing of broad whitefish has not been established. As the population segregates into the respective spawning stocks, the overall population is no longer exploited uniformly as it may have been in the pre-spawning aggregation sites. Now each spawning population is subjected to a different amount of fishing pressure. For example, the proportion of the individuals that migrate up the Peel River will be subjected to the fishing pressures associated with that migration. The remaining proportion of the migrating spawners will continue up the Mackenzie mainstem, Horse Shoe Bend area (Figure 8) until they reach the area of Point Separation where some of the individuals terminate their upstream migration and spawn (Chang-Kue and Jessop 1997 a). Once again, the remaining proportion of the individuals will continue their upstream migration, where some individuals will leave the Mackenzie River and enter the Arctic Red River and spawn at the Weldon Creek area on the Arctic Red River (Chang-Kue and Jessop 1997 a). Individuals which continue migrating up the Mackenzie River will terminate their migration at their spawning grounds in the Fort Good Hope area near the Ramparts Rapids, and be subjected to exploitation levels associated with this area (Chang-Kue and Jessop 1997 a, b, c). During these migrations to distant spawning areas, some spawners may separate from the main group of migrants and spawn at other locations within the larger rivers or in the mainstem Mackenzie downstream of Fort Good Hope. The locations and the existence of such areas is unknown at present.

After spawning the spent adults make their way from their respective spawning grounds downstream to overwintering areas in the outer delta (Baker and Reist 1988, Reist and Bond 1988). The downstream run is thought to be less concentrated and may last well into the winter with individuals reaching overwintering sites in the delta well into the months of January and February (Schmidt et al. 1989). The spent individuals then rejoin the resting or non-spawning population.

Broad whitefish are thought to possess a two year cycle of reproduction in which the fish rest at least one year subsequent to the spawning event (Reist and Bond 1988). This allows these fish to gain sufficient energy to create gametes and spawn once again. From the energetic costs associated with egg production it is assumed that females are more likely than males to rest for at least one, and perhaps more years. However, only small numbers of mature non-spawners have been reported from coastal habitats (Galbraith and Hunter 1975, Kendel et al. 1975, Bond 1982, Lawrence et al. 1984, Bond and Erickson 1985, Reist and Bond 1988). The failure to document significant occurrences of this resting segment of the population suggests that individuals remain widely dispersed or congregate in areas further inshore that have not been sampled (Reist and Bond 1988). Alternatively, there may be a higher incidence of consecutive-year spawning than is presently believed (Reist and Bond 1988).

Broad whitefish spawning behaviour is assumed to be similar to lake whitefish as described by Freeberg et al. (1990). Once the broad whitefish reach their respective spawning grounds they probably broadcast their eggs and milt on rock or gravel substrates, usually in relatively shallow water less than five meters deep.

It is the general aim in this work to develop a quantitative model of broad whitefish population dynamics. The model, BDWT 1, is based on a single stock

hypothesis because information regarding the differences between the proposed stocks is not complete. Wood et al. (1987) stated that it is not worthwhile managing a fishery on a stock-by-stock basis unless there is a clear difference between the stocks being managed. Also, a single stock design reduces model complexity, and reduces the number of parameters that need to be estimated from little or no information. As more information regarding stock structure becomes available, the basic model could be refined to include this complexity.

2.4 The Broad Whitefish Fishery

The fisheries for coregonids within the Mackenzie River system can be defined as subsistence or commercial fisheries. Subsistence fisheries include all domestic fishing by Indian, Inuit, or persons of mixed blood utilizing traditional methods to provide for themselves, their family or their dogs (Government of Canada 1978, McCart 1985). Subsistence fishing can also be defined as non-commercial fishing for the purposes of local food use by the harvesters, their families and community (Berkes 1988, 1990). Commercial fisheries include all fishing for sale or barter (Government of Canada 1978, McCart 1985). Commercial fishing also includes exploitation by test fisheries such as that conducted by the Inuvialuit. For the purposes of this model all exploitation by fishing, either subsistence or commercial will be summed and treated as a single incidence of fishing mortality.

The Mackenzie River, its tributaries, and the Mackenzie Delta host a variety of fish resources of which the Coregonidae are the most important (McCart and Den Beste 1979, McCart 1985). The major species are: broad whitefish, inconnu (*Stenodus leucichthys* (Guldenstadt)), Arctic cisco (*Coregonus autumnalis* (Pallas)), least cisco (*Coregonus sardinella* (Valenciennes)), and the lake whitefish (*Coregonus clupeaformis* (Mitchell)). Many of these species are

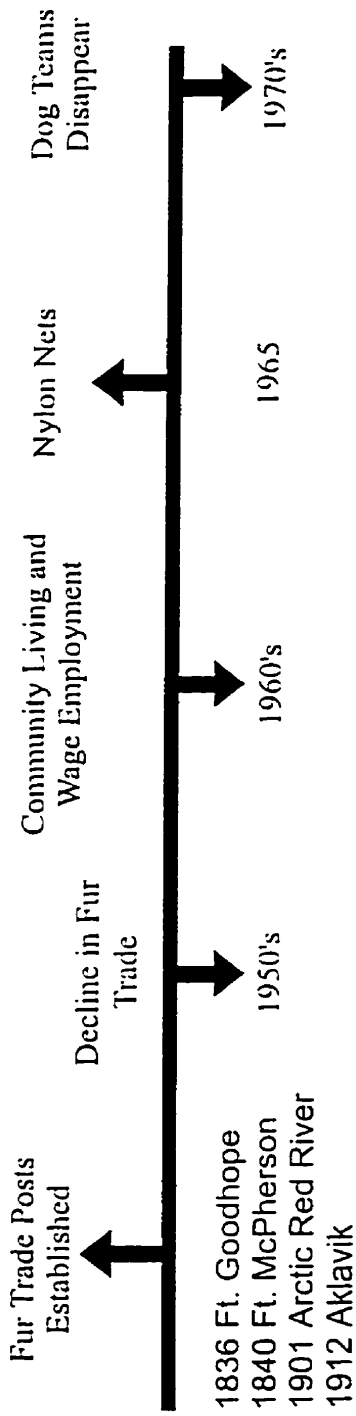
subject to both commercial and subsistence fisheries. The broad whitefish is heavily fished on a subsistence level and on a commercial level. The broad whitefish is one of the most desirable domestic fisheries in the Mackenzie Delta Region of Canada (Ratynski and de March 1989, Stewart 1996). Broad whitefish are valuable to subsistence fishermen because they are available at predictable times and locations and their flesh is free from *Triaenophorous crassus*, a tapeworm common to lake whitefish in the Mackenzie River. Their flesh is of high quality and regarded as being an excellent food fish that is an important part of the diet to the local people (Treble 1996).

The current subsistence harvest by aboriginal fishermen is unregulated and no quota or gear regulations have been imposed (Yaremchuk et al. 1989). Typically, fishermen use gill nets of 25 meters in length and a mesh size of 114 - 140 mm (4.5 to 5.5"). The fishing areas have been located in order to take advantage of the seasonal migrations of the broad whitefish, especially the pre-spawning aggregation which begins in July. Areas of exploitation are usually situated near a town site, along the mainstem of the Mackenzie River, or one of its tributaries (Figure 6). The following areas are major sites for exploitation - specifically: 1) the Peel channel of the Mackenzie Delta near the community of Aklavik; 2) areas near the community of Fort McPherson, located 30 to 40 km south of the confluence of the Peel River and the Mackenzie River; 3) near the community of Tsiigehtchic, located at the confluence of the Arctic Red River and the Mackenzie River; and 4) near the community of Fort Good Hope, located on the mainstem of the Mackenzie, below the Ramparts Rapids. Three areas of exploitation at more coastal locations are: Tuktoyaktuk Harbour, Whitefish Station, and Shingle Point (Treble 1996). The subsistence harvest is thought to compose approximately 80 % of the total harvest (Kg) in the Mackenzie Delta (Corkum and McCart 1981) but may compose 93 % of the total harvest (Kg) in

the Mackenzie Delta (Treble 1996). Heavy exploitation, both commercial and subsistence occur at the Horseshoe Bend area in the mainstem of the Mackenzie (Figure 8).

There have been several attempts to develop an export commercial fishery for broad whitefish in the Mackenzie Delta (Treble 1996) (Figure 9). The first commercial fishing venture began in the early 1900's. It involved the purchase of fish by the Anglican and Roman Catholic Missions, and the Royal Canadian Mounted Police (RCMP) from the local fishermen. These groups also hired local people to provide them with fish (Barlischen and Webber 1973). In 1950 a local entrepreneur used a ski-plane to commercially fish several outlying lakes within the delta (Treble 1996). The next commercial fishing venture occurred in 1960. The Department of Northern Affairs and Natural Resources (DNANR) ran fisheries at Aklavik, Kittigazuit, and the mouth of the Peel River. Equipment failures, in addition to inadequate freezers and storage space, terminated the fishery shortly after its inception (Barlischen and Webber 1973). In 1963 and 1964 a smaller commercial fishery was attempted by the Department of Indian and Northern Affairs (DIAND) at Holmes Creek (195 km north of Inuvik on East Channel). High processing and transportation costs and a poor local market caused this attempt to fail (Barlischen and Webber 1973). Fish Company of Edmonton hired local fishermen in 1965 and 1966 and operated a commercial fishery out of Inuvik. Mechanical problems with the processing and storage plant again discouraged further development after 1966 (Barlischen and Webber 1973). The Holmes Creek fishery was re-opened in 1972 with the objective of supplying the local-sale market (Treble 1996). During 1974 some of these fish were sold to the Freshwater Fish Marketing Corporation (FFMC) (Yarmechuk et al. 1989). Between 1975 and 1989 no commercial

FACTORS AFFECTING SUBSISTENCE HARVESTS



COMMERCIAL FISHING AND TEST FISHING VENTURES

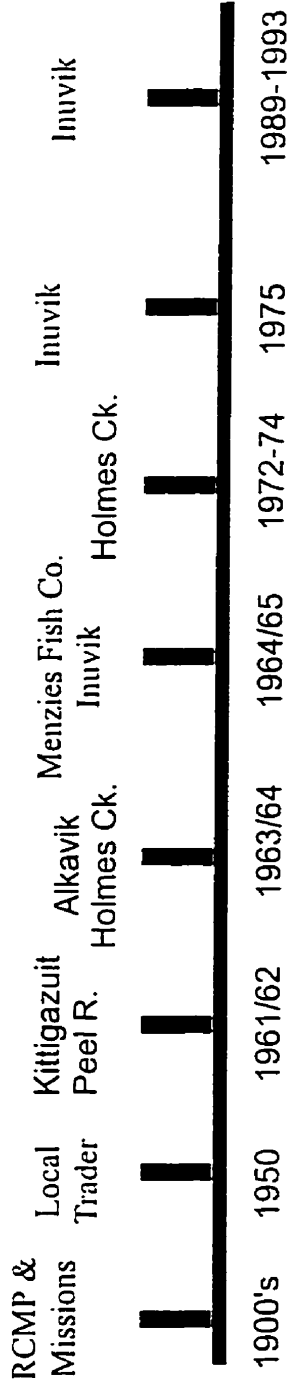


Figure 9. Harvest Trends over time in the lower Mackenzie River. Redrawn from Treble (1996a).

fisheries operated but some subsistence fishermen purchased commercial licenses to sell their excess subsistence catch in the local market (Treble 1996). In 1989 the Inuvik Hunters and Trappers Committee (HTC) started an exploratory broad whitefish fishery which ran for five years in the central delta (Figure 8). During the first four years fish were exported through the FFMC, and during the final year they were marketed in the Northwest Territories and the Yukon Territory by the Uummarmiut Development Corporation (UDC) (Treble 1996). Like previous attempts this venture proved to be unsuccessful due to problems with equipment, insufficient market value prices, and weather (Anderson 1995).

The commercial test fishery was prosecuted in much the same way as the subsistence fishery is today, with the same gear and technology being employed. However, it differed in the way the catch was collected. A single vessel from Inuvik (the "Northwind") travelled through the delta collecting the catch of each individual commercial fish camp. Waybills were produced for the catches and the product was readied for shipment to the Freshwater Fish Marketing Corporation in Winnipeg, Manitoba. This method of collection allowed the harvest to be quantified individually for each fisherman at each locale, providing accurate and reliable estimates of the catch.

Migrating broad whitefish can be exposed to different levels of fishing pressure depending on which spawning population a particular group of fish belongs. The migrating component of the population is the only portion of the population that incurs significant fishing mortality in any one year because fish migrate through areas of exploitation. During the winter months most fish are not in the vicinity of exploitation. Migrating fish may incur exploitation both before spawning during their upstream migration and after spawning during their downstream migration. In October and early November, mature broad whitefish migrate upstream to their spawning grounds with the greater part of this

migration occurring under the ice. The intensity of exploitation is greatest during the upstream migration (pers. comm. M. Treble). Tolerable weather conditions, the high quality of flesh provided by pre-spawning fish and the densely concentrated run cause local fishermen to expend most of their fishing effort during this time. During late November and December, inclement weather conditions, increased ice thickness, poor quality of post-spawning fish and a less concentrated downstream run cause fishing success to decrease relative to that of upstream run (pers. comm. M. Treble, K. Howland). Therefore, I have assumed that for any year about seventy percent of the total catch is obtained during the upstream migration and about thirty percent of the total catch is obtained during the downstream migration.

The level of exploitation and the number of times individual fish are exposed to exploitation depend on the route used to reach the spawning grounds. The set of equations below illustrates the various levels of exploitation that each of the four stocks is subjected to throughout their migration. The simulation model does not take into account separate stocks however, the equations below illustrate that migration can have a significant effect on exploitation levels.

The individual catches for the four major stock groups are:

Catch within { } only acts upon first time spawners

$$\begin{aligned}
 C_p &= \{C(\text{sp}) + C(\text{tk})\} + C(\text{hb}) + C(\text{mac}) & (2) \\
 C_a &= \{C(\text{sp}) + C(\text{tk})\} + C(\text{hb}) + C(\text{ar}) & (3) \\
 C_s &= \{C(\text{sp}) + C(\text{tk})\} + C(\text{hb}) & (4) \\
 C_g &= \{C(\text{sp}) + C(\text{tk})\} + C(\text{hb}) + C(\text{ar}) + C(\text{gh}) & (5)
 \end{aligned}$$

Where:

C_p = total annual average catch of broad whitefish belonging to the Peel River stock
 C_a = total annual average catch of broad whitefish belonging to the Arctic Red River stock
 C_s = total annual average catch of broad whitefish belonging to the Point Separation stock
 C_g = total annual average catch of broad whitefish belonging to the Fort Good Hope stock

and,

C(hb) = average annual catch of broad whitefish at Horseshoe Bend
C(sp) = average annual catch of broad whitefish at Shingle Point
C(tk) = average annual catch of broad whitefish at Tuktoyaktuk Harbour
C(mac) = average annual catch of broad whitefish at Fort McPherson
C(ar) = average annual catch of broad whitefish at Arctic Red River
C(gh) = average annual catch of broad whitefish at Fort Good Hope

Note that catches with the braces, {}, occur only upon the first-time spawners emerging from the lakes of the outer Delta and the Tuktoyaktuk Peninsula. The listing of the catch equations above is in increasing order of the distance of migration the particular stock undergoes between the coast and the respective spawning area, i.e., $C_s < C_a < C_p < C_g$. From equations 2 - 5 it is apparent that the number of exposures to a fishery and hence the amount of exploitation generally increases with the distance of migration. The Point Separation stock migrates the shortest distance and can be exploited a maximum of three different times. The Fort Good Hope population migrates the farthest distance and generally can be exploited as many as five times.

Due to the complex channeling of the delta system it is conceivable that there may exist a multitude of routes for migrating fish to use during their spawning migrations. The year-to-year variability of the route selection of a spawning stock may greatly influence the catch. This variability in route selection will also cause estimates of CPUE to be inaccurate or highly variable from year to year. The choice of route selection may be a chance event or the individuals may be forced to change routes due to the dynamic nature of the delta system.

The migration of fish from pre-spawning aggregation sites may actually be temporally stratified, each segment comprising a particular spawning population. It would be most logical to assume that individuals migrating to the Fort Good Hope site most likely depart from the pre-spawning aggregation sites first, since they have the farthest distance to travel. Following this logic, the Peel River population, Arctic Red River population and finally the Point Separation

population would follow them. If these generalities were followed strictly and if accurate measurements of the timing of these migrations could be made, this would provide managers with an important piece of information. The level of exploitation each stock suffers could be managed by regulating the level of effort expended by fishermen during a particular stock's migration period. However, these temporally segregated movements are not always carried out as outlined. Radio-tracking studies show instances where fish depart from pre-spawning aggregation sites late in the year yet migrate to the furthest spawning site (e.g., Fort Good Hope) (Chang-Kue and Jessop 1997a, b, c). In this case fish must migrate upstream at a greater velocity to make up for their late departure time (Chang-Kue and Jessop 1997a). This behaviour could create problems when trying to manage the population on a stock-by-stock basis. Data would have to be collected for each stock separately, and the delta fisheries would have to be managed using a mixed-stock fishery model. Our current knowledge regarding the system and its resources, in particular the differences between separate stocks prevent managing this fishery using a mixed-stock fishery approach. It is necessary to completely understand and quantify the difference between separate stocks in a fishery but a significantly large difference must exist between stocks in order for a mixed-stock fishery approach to be used effectively (Wood et al. 1987). To avoid unnecessary complexity in the model, and because information that illustrates significant differences between stocks does not yet exist I have developed the model as a single stock model.

2.5 Population Regulation Mechanisms

An essential feature of any fishery is the dynamics of the population. Patterns of fecundity, mortality, dispersal, degree of intra- and interspecific competition, and species richness depend upon the population dynamics of a system (Winemilller and Rose 1992). If the population dynamics are understood, predictions about birth, death, growth, and movement processes of the fish can be made (Hilborn and Walters 1992). A simple conceptual model shown in Figure 10 can describe the population dynamics of any population. It shows typical inputs into, and outputs from, the population. Recruitment and growth cause the population to grow in biomass. Common outputs such as fishing mortality and natural mortality cause the population to decrease in biomass. The model developed herein, BDWT 1, attempts to model the essential components that describe the dynamics of the migratory population of broad whitefish in the lower Mackenzie River.

Mechanisms responsible for regulating population abundance must be studied in order for a fishery to be successfully managed. Fishery scientists must understand the mechanisms controlling growth and survival during the early stages of life (Gulland 1965). Early life mortality, including that of the egg and juvenile stages, results from complex biological processes (Viljanen 1988). The time between spawning and recruitment to the adult stock involves a natural series of complicated pre-recruit events, including egg laying, hatching, metamorphosis, larval growth, survival in the nursery areas, and migration to adult feeding grounds (Megrey and Wespestad 1989). Prediction of recruitment from the egg to the adult stage of the life cycle is difficult and sometimes intractable. A better understanding of the web of ecological relationships surrounding the early life stages is required before recruitment can be satisfactorily predicted (Viljanen 1988). During development from egg to adult,

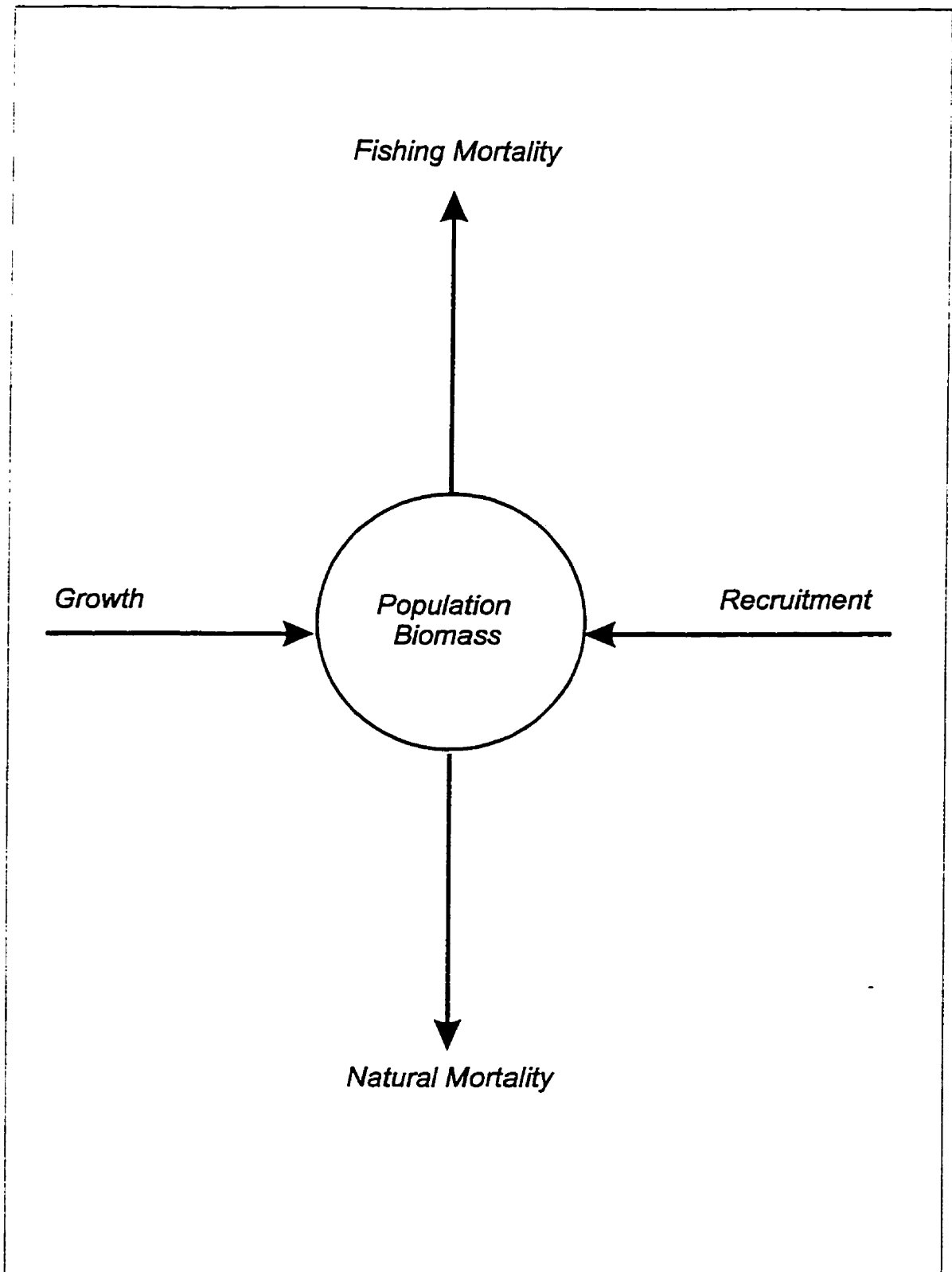


Figure 10. A fundamental model of fish stock population dynamics.

mortality can exceed 99.9 % for some freshwater fish (Hjort 1914 as cited in Viljanen 1988). Most of this mortality will occur in the early stages of the life cycle. Therefore, early life mortality likely plays a central role in regulating recruitment or adult population abundance. Mortality can be dependent on the number of animals in a population (density-dependent mortality). This occurs when mortality rates increase with increasing population levels. Mortality can also be independent of the number of animals in a population (density-independent mortality). This occurs when mortality rates fluctuate independently of population size.

Density-independent processes can play a significant role throughout the entire life cycle of the Mackenzie River Broad Whitefish (Reist and Chang-Kue 1997). Density-independent processes are usually random or chance events that may occur to increase the mortality of juvenile or adult fish, therefore play an especially important role in regulating population abundance during early life stages. Rotschild (1986) suggested that density-independent control of populations has the greatest effect during egg and larval stages. Major density-independent factors contributing to year-class strength are: over-wintering survival of juveniles, egg survival, amount of larval food available, timing of spring breakup, flow, volume, and river discharge (Sheperd and Cushing 1981, Bohling et al. 1991, Freeberg et al. 1990, Reist and Chang-Kue 1996). Thus, indirectly such physical parameters may have a significant impact on year-class strength and survival of the broad whitefish. Similar density-independent factors in the Baltic Sea, such as water temperature, wind, ice cover, water level, and human stresses such as pollution, are all suggested to be the main reason for the variability of coregonid recruitment in that area (Helminen et al. 1993, Lehtonen et al. 1995). Many authors have demonstrated sources of population variability among coregonid fishes. A general assumption is that both

recruitment and growth rate in northern latitudes are highly dependent on climate and other environmental factors (Van Winkle et al. 1978, Hannesson 1986, Salojarvi 1992 a, b). Density-independent control apparently becomes less important as fish enter the juvenile stages of the life cycle, i.e., become older.

Density dependence is the primary mechanism constraining major excursions in population density and keeping populations within bounds, but within those bounds density-independent phenomena predominate (Hughes 1990). Density-dependent control can take place during any of the life stages but density independent mechanisms are likely most prominent during the juvenile stages (Rotschild 1986), (Figure 11). Because juvenile broad whitefish inhabit a unique complex system, rearing in confined areas (freshwater lakes on Richard's Island and the Tuktoyaktuk Peninsula) that are limited in space and food, I assumed density-dependent mortality of young fish (ages zero to five) to be a chief mechanism regulating population abundance in addition to density independent effects. Viljanen (1988), Freeberg (1990), and Salojarvi (1992 c,d) all indicated that density dependent processes play a vital role in regulating coregonid populations. Evidence of density-dependent mortality in similar environments was shown by Tonn et al. (1994): Working on arctic tundra lake systems in Finland. Tonn et al. (1994) found that starvation-induced mortality, cannibalism, and crowding into unfit overwintering areas affected the dynamics of carp populations. The summer feeding period for the broad whitefish allows adequate storage of fat reserves that are important to ensure survival over the long winter (Fechelm et al. 1992). The inability of fish to increase their condition due to density-dependent phenomenon, such as competition for food during summer, could lead to higher winter mortality. Density-dependent growth is assumed to have the same effect as density-dependent mortality because density-dependent growth produces density-dependent survival (Sheperd and

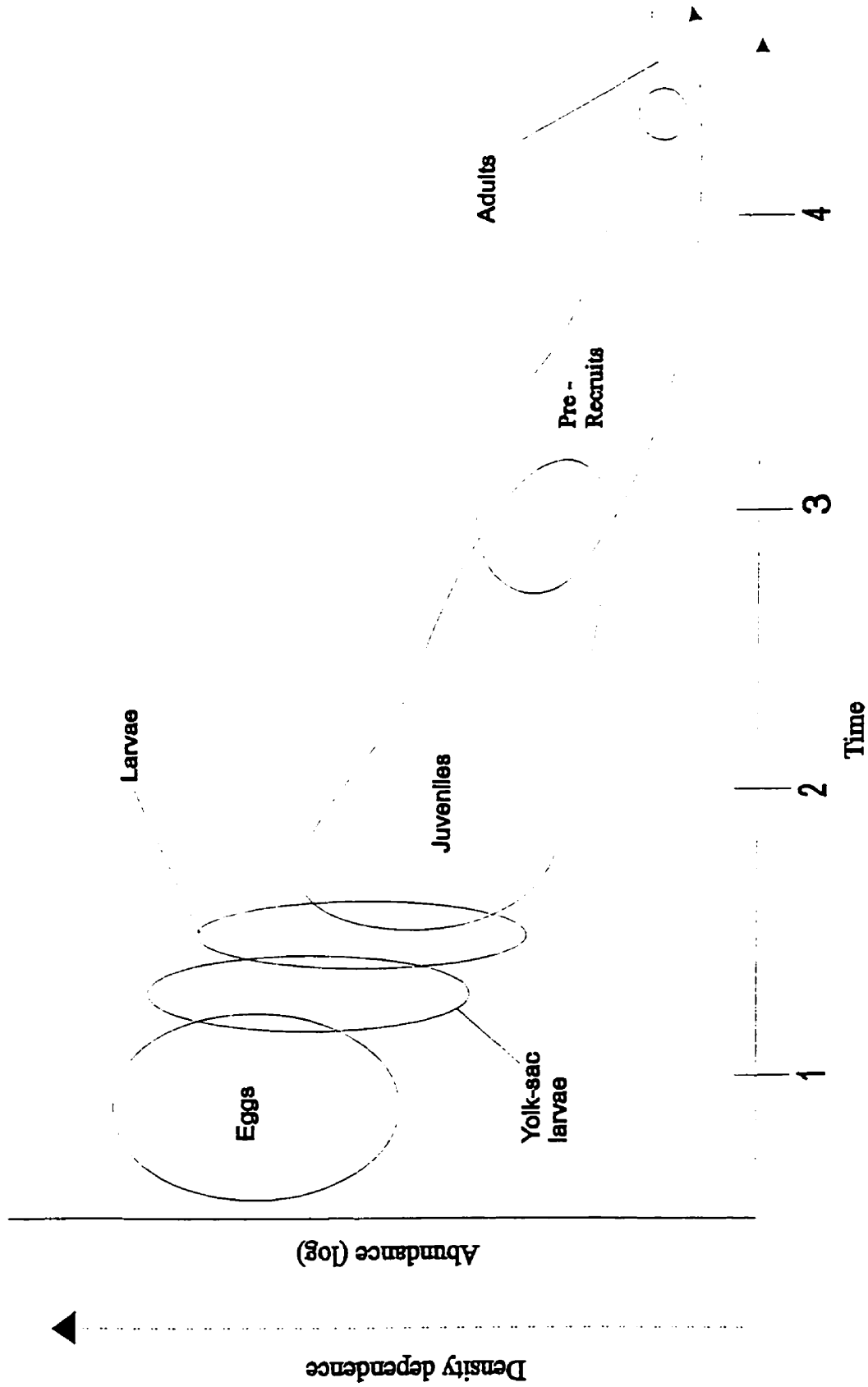


Figure 11. A conceptual model of the recruitment process in whitefish (after Salojoarvi 1992a).

Cushing 1981). Tonn et al. (1994) also indicated that density-dependent growth can result in density-dependent mortality, because juveniles that grow slower at high densities will remain more vulnerable longer to size-limited piscivores. As well, smaller individuals may also be forced into unsuitable over-wintering habitats. Lake whitefish have been observed to exhibit density-dependent growth, mortality, and recruitment (Jensen 1981, Salojarvi 1992d). Fish stocks with varying population densities such as the Mackenzie River broad whitefish population, likely exhibit density-dependent responses with regards to growth, age structure and recruitment due to intra-specific competition similar to other whitefish populations (e.g., *C. lavaretus*, Klein 1992). Intense competition for food and/or overwintering habitat may occur between young and older fish, or between fish of the same age (Salojarvi 1992c). Density-dependent mortality may also play a significant role in regulating population abundance during the juvenile stages if juveniles exhibit territorial behaviour in their rearing grounds. LeCren (1973) and Gee et al. (1978) found that the most likely process regulating population abundance in salmonids was density-dependent territorial behaviour. Evidence of juveniles exhibiting density-dependent territorial behaviour has been shown by Elliott (1990a) for brown trout and by Tonn et al. (1994) for carp. Since little is known about the behaviour of broad whitefish it is possible that this territorial behaviour exists.

Density-dependent mortality is regarded to be a necessity during some stages of the life cycle (Jensen 1981, 1989, 1993). It allows the population to remain stable and if the adult population is perturbed the population can respond or compensate for the perturbation by adjusting the rates of density-dependent mortality. Density-dependent mortality is caused by whitefish preying on their own offspring as eggs, larvae or juveniles, or through the competition for resources such as food and habitat (Salojarvi 1992c). Mortality that occurs

during larval or juvenile stages and variability of age-at-maturity were identified as factors with a potential for compensatory effects at the population level (Jensen 1989, 1993).

Compensation is the ability of a population to respond to perturbations in order to maintain a stable state (Healey 1975). The role of compensation is of central importance to fish populations because no natural population can persist for long periods without compensatory ability; the persistence of fish populations is strong evidence that compensation does occur (Sissenwine 1984, Rotschild 1986). Density-dependent compensatory processes cause mortality to increase and reproduction to decrease as the population size increases. This is the opposite of density-dependent depensatory processes, which cause mortality to decrease and reproduction to increase as the population size increases. Processes that contribute to compensatory mortality operate principally in juvenile stages of the life cycle rather than on the mature stock. Compensatory mortality is of greatest importance as a regulator of population size (Ricker 1975).

In this study, I make assumptions (e.g., density dependence, mortality rates, growth rates, and reproductive rates) about the population regulation mechanisms that operate on broad whitefish in the Mackenzie River Delta system. The assumptions are based on population regulation mechanisms operating on other species in similar systems. The assumptions may not reflect the actual mechanisms that operate in this particular system, but the importance that each mechanism plays in each stage of the life cycle of the broad whitefish can be realized.

2.6 Conclusion

The above background information on the physical setting, biology, the fishery and major mechanisms involved in regulating the size of the population is used to formulate a conceptual model, labeled herein as BDWT 1. The model represents the system in an abstract form taking into account what is assumed to be the most important components in the life cycle of the broad whitefish and its interaction with the subsistence and commercial fishery.

CHAPTER THREE

MODEL MOTIVATION AND DESCRIPTION

Section 3.1 Model Motivation

This study began as part of a project funded by the DFO/Inuvialuit Fisheries Joint Management Committee (FJMC), which represents the interests of the beneficiaries in the Inuvialuit Settlement Region (ISR). The FJMC recommends harvest quotas for commercial fishing, monitors fish harvests and advises the Minister of Fisheries and Oceans on all aspects of fishery management within the ISR (Stewart et al. 1993). The subsistence fishery for the Mackenzie River broad whitefish is one of their most important management concerns. The FJMC and the Department of Fisheries and Oceans (DFO) have committed themselves to ensuring the social and cultural way of life surrounding the subsistence fishery for broad whitefish will continue. In addition to this goal, the two organizations (FJMC and DFO) work together to properly manage a developing commercial fishery for broad whitefish. In order to accomplish these objectives, a better understanding of the broad whitefish resources in the Mackenzie River system must be obtained. From the scientific perspective, this may be achieved by: 1) implementing a research framework that represents our understanding of the system; and, 2) identifying where research should be focused in the future in order to obtain the maximum amount of benefits.

A systems analysis approach is used to represent all the available information collected on this population in a conceptual framework. The model attempts to assemble the essential components that describe the dynamics of this population in a simplified fashion. However, the model is structured in order to be able to take into account more complicated relationships as they become known. In the future this model should provide a clear definition of research

objectives and provide the framework for the analysis of policies concerning the management and development of the fisheries in this area. A study of this type on the Mackenzie River broad whitefish resources should not be delayed because the scale and complexity of the problem will require many years of focused research before the stock dynamics are clearly understood (Stewart 1996).

The Mackenzie River Delta can be regarded as a very complex geographical system. The management of its fisheries may prove to be an intractable problem. The complexity involved in the biology of the individual species, and their migratory behaviour make management of this resource extremely difficult. In addition to these problems, the creation of new political boundaries, and the threat of a large-scale export fishery being developed in addition to an already large subsistence fishery add further complexity to the problem. Because we are dealing with such a complex problem with limited amounts of time and research funding, a systems analysis approach may prove to be very useful. A modeling approach will also reveal contradictions or gaps in our knowledge, and point some ways possibly useful in overcoming problems in the future. Though a modeling approach can be useful tool in studying a complex problem by representing complex processes in a simplified fashion, a model can never represent the real world perfectly, regardless of the amount of knowledge we can obtain. The ideal situation is to construct a model that is complex enough to take into account all major interactions but still remains as simple as possible. This balance of complexity and simplicity is shown in Figure 12. The model, BDWT 1, was designed to achieve a balance between complexity and simplicity.

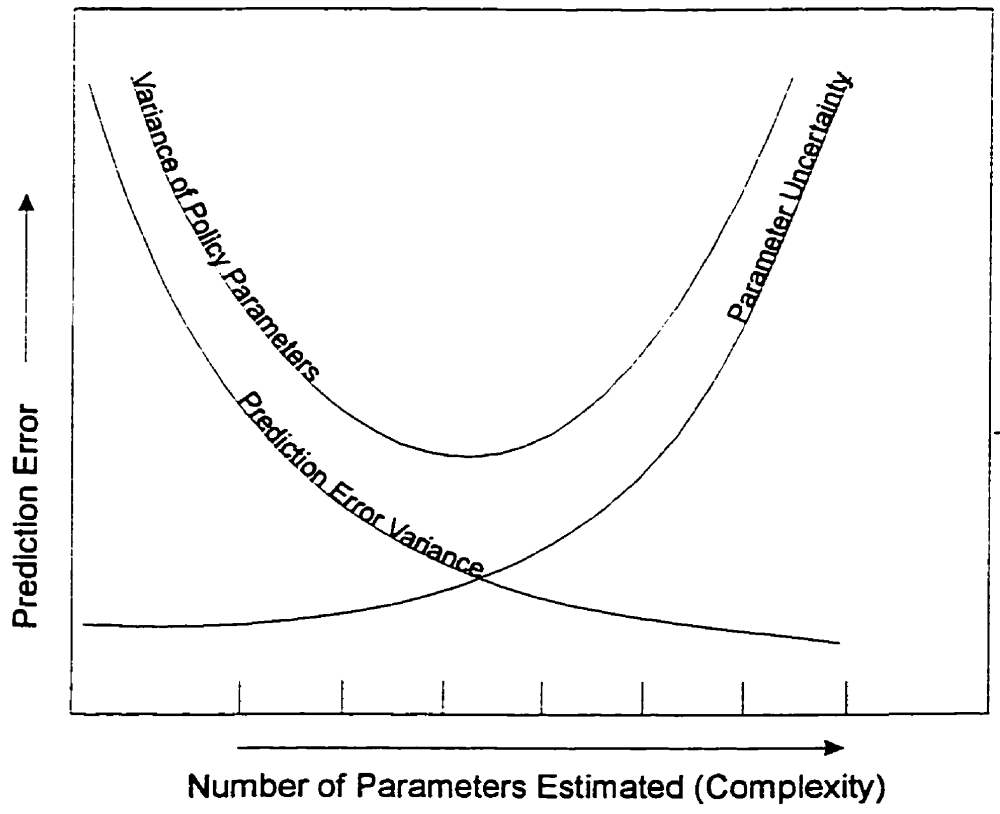
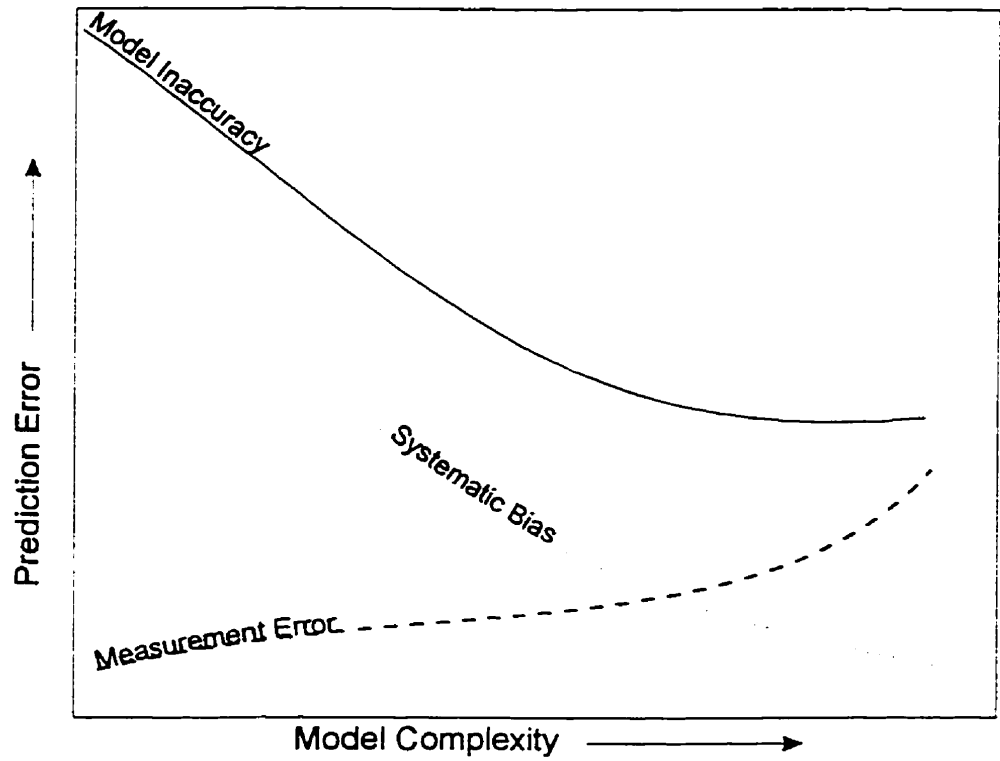


Figure 12. Determinants of optimal model size. Above figures illustrate the balance between model simplicity and complexity (redrawn from Hilborn and Walters 1992).

3.2 Systems Analysis and Simulation

A systems analysis approach was adopted for this study for four reasons.

1) The Mackenzie Delta is a highly complex system, and any attempt to quantify the fish resources of this area in order to define a quota would prove to be a mathematically intractable problem. 2) Management policies would have to be implemented for several seasons before their effects would become noticeable to fishery managers. By using simulation techniques, results from new management policies, based on the conceptual system, could be collected in seconds, giving managers an idea of the effects their decisions may produce in the future. 3) Also, by using simulation any management policies that may prove to be harmful to the resource can be thoroughly studied and eliminated before being used in the real world system, where mistakes could have irreversible effects. 4) Due to the location, size, and climate of the area it is very costly to do research. Simulation experiments can be performed for less than a fraction of the cost of experiments performed in the real world, yet still provide useful direction both with respect to management action as well as to the types of research necessary.

3.3 Model Construction

3.3.1 Problem Formulation

The fundamental biology and behaviour of the broad whitefish in the lower Mackenzie River is not well known. Some information has been gathered from a variety of studies since the early 1970's. The complex life cycle and population dynamics of the broad whitefish in the lower Mackenzie River pose a problem for fishery managers trying to manage the large subsistence fishery for broad whitefish. The potential for a large export commercial fishery for the broad whitefish intensifies the problem.

The purpose of the model is to bring all the available information together into a sound conceptual base where current hypotheses about the system can be explored using simulation. Once all the relevant information describing this system is together, gaps in our knowledge can be identified. Future research can then be focused toward supplying information that would minimize the deficiencies in our knowledge. Also, the model will facilitate the education of other professionals about this particular system. This will ensure management objectives and knowledge are maintained and passed on from various professionals who work on the system over time.

In the model several assumptions are made in the absence of information describing particular processes (Table 1). These assumptions are explained and supported with personal observations, evidence from supporting literature, collections of professional opinions, or experimentation with the model. Assumptions made throughout the model are dealt with in the section entitled model description.

The desired solution of the model will be involved with the identification of sensitive parameters. Furthermore, the process of constructing the model should have clearly laid out all the available information describing the system and thereby identifying areas where information is lacking.

3.3.2 System Definition

A method of collecting expert opinion, the Delphi-Technique (Zuboy 1981), was used to attain an estimate of the number of adult broad whitefish inhabiting this system. This allowed the input parameters of the model to be tuned to a range of population sizes that are reasonable for this system. In the model there are 14 input parameters (Table 2). They are denoted from P1 through to P14.

Table 1. Major Assumptions Made in the Model

1. Larval broad whitefish require 60 days to travel from their spawning grounds to their rearing grounds.
2. Density dependence occurs in the rearing grounds due to limitations in space and resources.
3. Post-spawning mortality is assumed to occur due to the large amounts of energy required to complete a spawning run in addition to mortality accounted for by fishing mortality. The level of post spawning mortality is assumed to be low due to the proportionate amount of pre-spawners and post spawners observed during migrations (Tallman unpublished data).
4. Resting overwintering adult mortality is set at 15 %.
5. The majority of fishing pressure is associated with the upstream pre-spawning run (70% on average).
6. Approximately 80 % of the larvae that hatch on the spawning grounds will reach the rearing grounds (freshwater lakes on the Tuktoyaktuk Peninsula).
7. The remaining 20 % of the larvae will find their way into less suitable habitats such as the delta lakes where they will experience severe mortality (approximately 80 %).

Table 2. List of model parameters, definitions, values and their sources.

	Symbol	Description	Mean Value	Variation	Source
P1	fecund	number of eggs produced per female	44261	S.D. = 14839	Chudobiak 1996
P2	eggs	eggs produced from population that will have a chance to hatch	B/H eq.	+/- 10%	Ricker 1975 & calibration
P3	ssr	level of egg survivorship	90%	+/- 10%	Elliott 1985 and Bogdanov 1991
P4	larvaeT	larvae that become trapped in delta lakes	20%	+/- 10%	Reist and Bond 1988
P5	M1r	Mortality level that larvaeT will encounter	80%	+/- 10%	Lawrence et al. 1982 + assumption
P6	Daily Mr	daily mortality incurred during downstream migration of larvae	10%	+/- 10%	Bogdanov 1991
P7	JYXA	Juvenile density dependent parameter in tundra lakes	function		Assumption - function derived w/ D. Gillis and Maple 4.0
P8	JYXB	Juvenile density dependent parameter in tundra lakes	function		Assumption - same as above
P9	F1	Level of coastal fishing mortality	0.1	+/- 20%	Treble 1996a and Freeman (1997)
P10	F2	Level of delta fishing mortality	0.15	+/- 20%	Treble 1996a and Freeman (1997)
P11	F3	Level of pre-spawning fishing mortality	0.25	+/- 20%	Treble 1996a and Freeman (1997)
P12	70/30 spl	Ratio of upstream vs. downstream fishing mortality	70/30	+/- 20%	Personal Communication (J. Reist, K. Howland, D. Chudobiak)
P13	psm	post spawning mortality	5%	+/- 5%	Tallman (unpublished data)
P14	owm	Natural or overwintering mortality	15%	+/- 10%	Healey 1975

Model outputs are adult population size, a measure of the sensitivity of the parameters and interactions between them, and an exploration of the relationships between exploitation and population size. The performance criteria used is the model's ability to identify important information deficiencies and its ability to produce population sizes similar to the expected sizes and to produce expected exploitation levels at sensible values of fishing mortality.

3.3.3 Conceptual Model Formulation

Attributes of the physical system, behaviour of the broad whitefish and the fishermen throughout the lower Mackenzie River system were represented conceptually in a flow diagram (Figure 13). Processes that could not be explained by the literature were interpreted either with the help of expert opinion or from comparisons made from other systems. Specific methods used to collect or assign values to input parameters are shown in Table 2.

3.3.4 Model Data Preparation

Input data that facilitate the determination of exogenous parameter values, and define data for model initialization are needed. Using the Delphi - Technique (Zuboy 1981), a consensus of expert opinion of the adult population size of broad whitefish in the Mackenzie Delta was determined. Eight experts were asked their opinion on the minimum, modal, and maximum values of population size, and a distribution describing the size of the adult population was created.

Estimates of fecundity were obtained by empirical measurements of fecundity (number of eggs per female) for the Arctic Red River stock by Chudobiak (1996). The average fecundity for this population was estimated at 44, 257 eggs per female with a standard deviation of 14, 840. de Graaf and Machniak (1977) reported fecundity estimates ranging from 26, 922 to 65, 798 with a mean value of 39, 721. The difference between these two means was

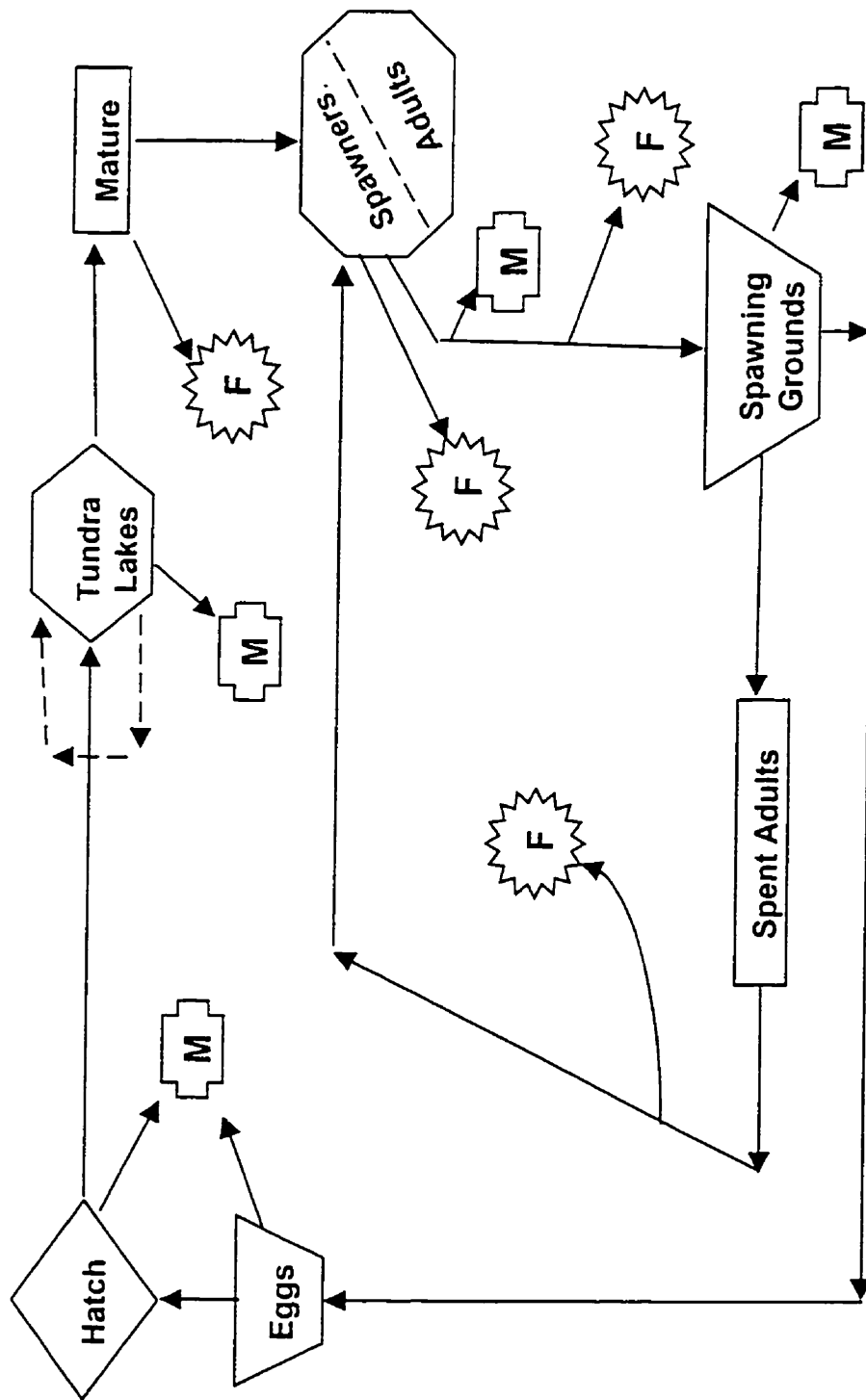


Figure 13. The conceptual model of BDWT 1, illustrating the sources of natural (M) and fishing mortality (F) throughout the life-cycle of the broad whitefish.

tested using a two tailed t-test at an alpha of 0.05 as described in Sokal and Rohlf (1995). This test indicated that there is no significant difference between these two means (Table 3). Due to the fact no significant difference between the two population means could be detected, a measure of variance could be obtained, and fish contained in the sample were from the same population the model emulates, Chudobiak's fecundity data was used in the model.

To account for the variability in fecundity among spawning stocks during a particular year due to size, age, or energy acquisition, the value of fecundity was made stochastic. The value used was chosen randomly from a normal distribution with a mean of 44, 257 with a standard deviation of 14, 840 eggs per female during each repetition of the model. In order to ensure that this would be an accurate representation of the fecundity data, the data were tested for normality using an R-J test (Figure 14).

It is also assumed that there is a limited number of eggs that can be successfully fertilized on the spawning grounds (Equation 7). Of the eggs that were successfully fertilized it is estimated that 90 % will hatch. This value was obtained from literature sources describing the hatching success of broad whitefish and other similar species. Bogdanov et al. (1991) state that the success of hatching of the Man'ya River broad whitefish was estimated to be 90 % or greater. His work in the Man'ya River of the Lower Ob Basin showed that there were few dead eggs in the downstream migrations of the larvae. Since these estimates of survival were based on the number of dead eggs present in drift nets downstream and the fact that many of the dead eggs will not be mobile in the water column, Bogdanov's (1991) estimates may be inflated. However, Allen (1958) found by direct inspection of spawning sites that mortalities of

Table 3. Descriptive statistics from two independent calculations of fecundity for the Mackenzie River broad whitefish. t-Test indicates no significant difference between the two population means.

	Chudobiak (1996)	de Graaf and Machniak (1977)
Mean	44257	39721
Standard Deviation	14840	*13038
Median	45322	n/a
Minimum value	18375	26922
Maximum value	69007	65798
sample size	n = 18	n= 11

*estimated

Results from the t-Test exploring the difference between two means:

t (observed) = 2.130

T(critical) = 3.038

since t(obs.) is < T(critical) we conclude that the means from the above two populations are **not** significantly different.

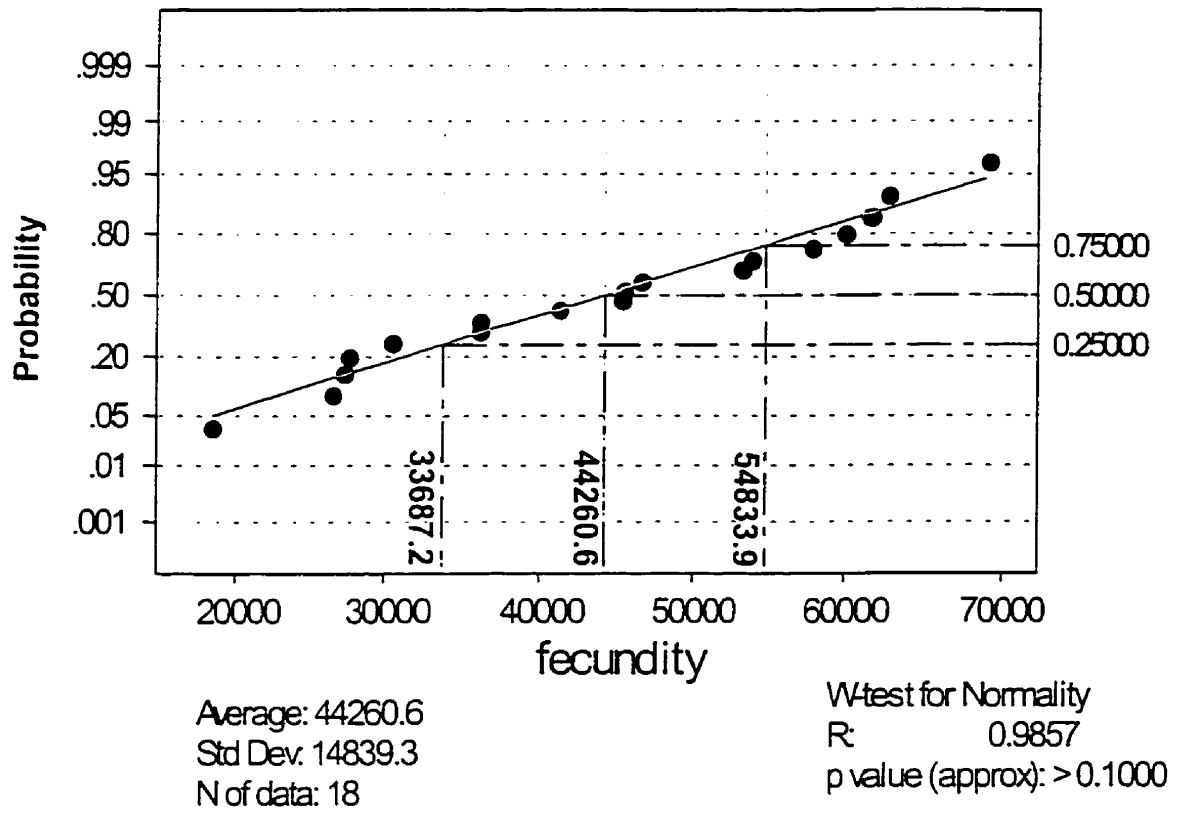


Figure 14. A normal probability plot indicating test results from a Ryan-Joiner (R-J) normality test. Test indicates that the fecundity data used in the model conform well to a normal distribution.

Pacific salmon were 10 % or less, (i.e. 90 % + survivability). Studies on brown trout (*Salmo trutta*) indicated egg mortalities as low as 8 % in the wild and 11 % in the laboratory (Elliott 1984, 1989). The above literature suggests that an egg survivability value of 90 % is a logical estimate and therefore a relatively high amount of confidence can be placed in the estimation of this parameter.

In nature, egg survival, likely fluctuates due to seasonal variability including catastrophic events on the spawning grounds. Therefore, the value for egg survivability was chosen randomly from a normal distribution with a mean of 90 % and a standard deviation of 3 %. Because the literature values suggest a narrow range for this parameter, the value for the parameter will be chosen between the range of 99 % and 81 % a total of 99.5% of the time.

In the model, larvae were divided into two groups. The division of larvae into two groups was based on information in the literature indicating that < 10% of the larvae reach rearing habitats on the Yukon coast with an additional 10 % residing in delta lakes (Reist and Bond 1988, Bond and Erickson 1985). It was assumed that 80 % of the larvae composed the group which migrates downstream to rearing grounds on Richard's Island and the Tuktoyaktuk Peninsula and the remaining 20 % of the larvae composed the group which become trapped in delta lakes to overwinter. This assumption was based on literature qualitatively describing the proportion of larvae that suffer either fate (Reist and Bond 1988, Bond and Erickson 1985). The ratio will vary seasonally due to chance events controlling the proportion. This variability was represented stochastically by choosing a percentage of larvae that will migrate downstream from a normal distribution with a mean of 80 % and a standard deviation of 6 %. This level of variance is used to represent the natural variability in this process in the absence of empirical data (Hagiwara and Mitsch 1994). The mean ratio of

80:20 is believed to be adequate for the purposes of this model given our knowledge about this process.

Each of the above groups of larvae experience different rates of mortality in the conceptual system. The group of larvae overwintering in the delta lakes (20 % of total larvae) was assumed to experience annual mortality levels of 80%. This high level of mortality was selected because delta lakes have been shown to be poor overwintering habitat for juvenile broad whitefish (Taylor et al. 1982). Many lakes become anoxic or freeze to the bottom over the winter months thus precluding survival. The lakes that remain suitable for overwintering are abundant with predators like northern pike (*Esox lucius*) and burbot (*Lota lota*) (Taylor et al. 1982).

The larger group (80 % of the total larvae) was estimated to experience between zero and 10 % daily mortality during their 60 day journey downstream (Bond and Erickson 1985, Chang-Kue and Jessop 1992, Bogdanov et al. 1991). Mortality was considered to be highly variable due to seasonal variation and the occurrence of catastrophic events such as ice jams. The level of mortality was chosen stochastically during each time step of the model from a normal distribution between 0% and 10% with a mean of 5%. The reliability of this parameter should be high because it was estimated from work done with broad whitefish in the Man'ya River by Bogdanov et al. (1991).

Juveniles in their rearing grounds (tundra lakes) were assumed to experience density-dependent mortality. This assumption is the most crucial assumption in the conceptual system. The form of the function was chosen to represent density-dependent mortality in the conceptual system over other functions (Ricker, Beverton-Holt), because it required the fewest number of parameter estimations. Also, during stress testing it operated logically over a wide range of adult population sizes (i.e., 1 - 20 million), unlike the two other

functions that were tested. Parameter “K” in equation represents the amount of natural mortality in addition to the density-dependent mortality occurring on that particular group of fish. Parameter “K” was assumed to equal 15 % and guarantees that under extremely low densities (density independent) juveniles experience mortality rates of 15 %. The most sensitive parameter in this function is “m” which governs the level of mortality larvae will incur. The parameter “m” was tuned in order to achieve mortality levels that decrease by 10% for each successive age group of fish from zero to five. After the age of five “m” becomes fixed. This parameter was validated using a technique called face validity which involves questioning experts on the legitimacy of the assumption, reasonableness of the parameter value, and the correspondence of the model output to the natural system. This parameter was obtained with the least amount of empirical data and unfortunately it was the most sensitive parameter in the model. In order for our confidence to improve regarding this parameter, a more reliable estimate of population size must be obtained as well as empirical data describing the density-dependent mortality in the rearing grounds. Confidence in the predictive ability of this model can only be as high as confidence in the most sensitive parameter, thus this is a limiting factor for the model. The level of instantaneous fishing mortality (F) was estimated from catch curves produced from the commercial fishery in Horseshoe Bend for the years 1989 through and including 1993 (Treble and Tallman 1997). Levels of catch for 1955 to 1993 were estimated from reports outlined in Treble (1996), (Figure 15). Harvest levels are separated into three distinct areas of exploitation: Coastal, Delta, and Pre-spawning Areas (Table 4).

Treble (1996) obtained subsistence and commercial values of catch through the collation of past reports that document harvest during the years 1955 to 1993. Many of the reports did not differentiate between species.

Total Reported Harvest of broad whitefish in the lower Mackenzie River region, 1955-1993.

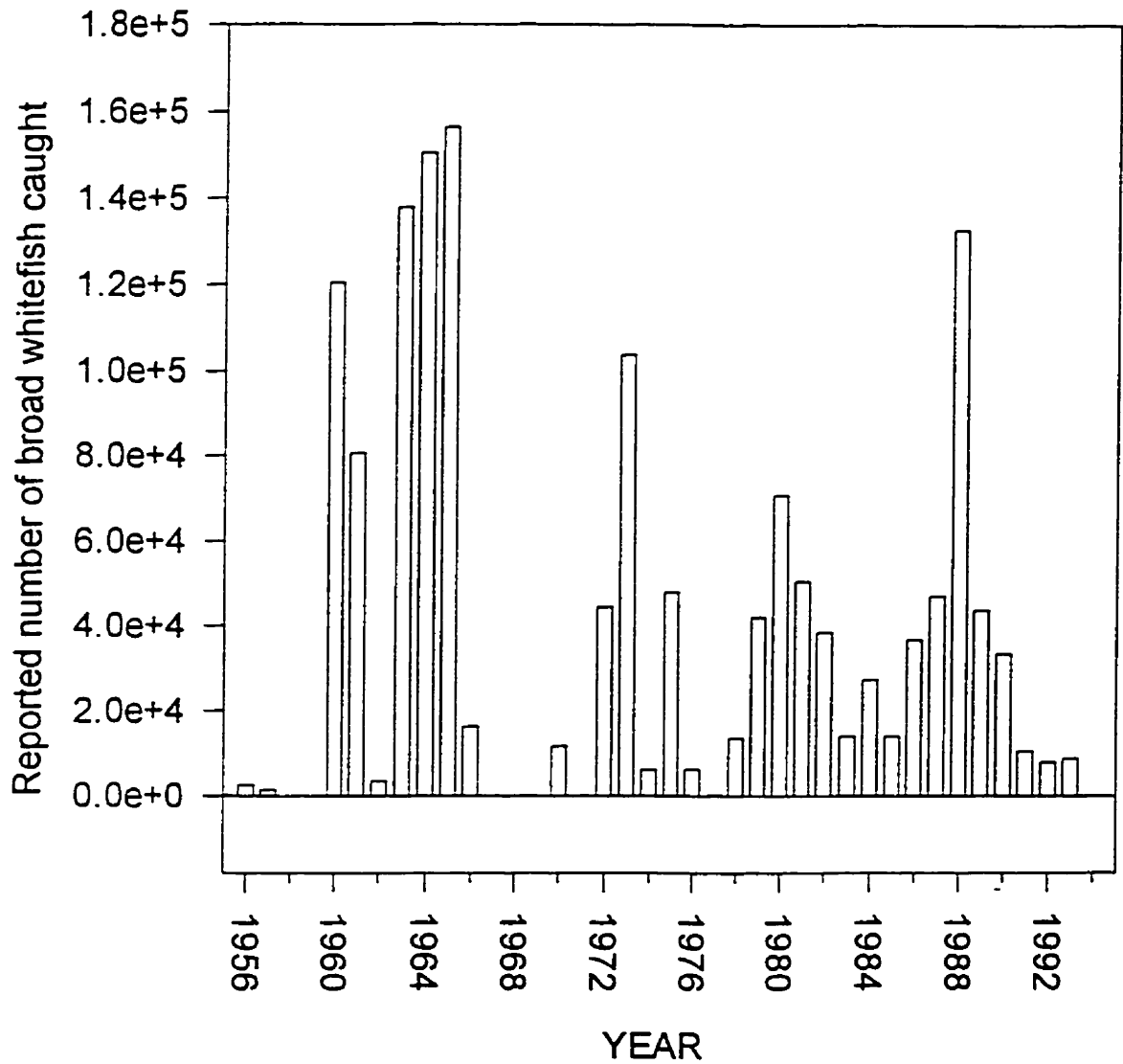


Figure 15. Total combined reported harvest of broad whitefish in the lower Mackenzie River region during 1955-1993. Estimates based on data from subsistence, domestic licence, and commercial sales. (Treble 1996).

Table 4. Annual levels of catch of broad whitefish for the Mackenzie River system calculated from harvest data from 1955 to 1993. Summary statistics (mean, standard error, median, standard deviation and variance of catch for all 3 locations. Estimated from Treble (1996).

Coastal		Delta		Pre-spawning	
Mean	9720	Mean	59769	Mean	27950
S. E.	4227	S. E.	15900	S. E.	7636
Median	766	Median	11038	Median	859
S. D.	27068	S. D.	101808	S. D.	48897
Variance	732654998	Variance	10364819861	Variance	2390945936

Commercial harvest totals were estimated using the assumption that sixty-seven percent of the catch reported as whitefish spp. were broad whitefish and subsistence harvest totals were estimated under the assumption that thirty-five percent of the total catch was composed of broad whitefish. These estimates were validated by calculating the percentage of broad whitefish contained in catch records, where records indicated differences between species in both commercial and subsistence reports. Reports that documented harvest in kg of fish were converted to numbers of fish using the conversion factor of 2.3 kg per fish (Treble 1996a). For instances where more than one report existed for a certain year, the report documenting the highest harvest value was used.

The validity of the results from Treble (1996) depends mainly on the accuracy of the original reports. Previous reports obtained most information on catch levels by using recall interviews with fishermen. The fishermen being interviewed may not be able to recall accurately how many fish have been harvested or he may consciously bias his estimates high (to boast of his fishing ability) or low (to prevent regulations from being imposed). Catch levels reported by Treble (1996) are valuable because harvest levels are obtained from many areas throughout the delta including all land claim areas and represent the first comprehensive attempt to estimate the total harvest of broad whitefish throughout the entire lower Mackenzie River basin.

Comparing catch values that were estimated by the traditional knowledge study conducted by Freeman (1997) validated this information describing catch. Freeman (1997) used interviews of local elders to obtain information regarding the average number of days fished (D), the average daily catch per house (C), the proportion of catch that was broad whitefish (P), and the number of households in the community (H). The following formula was applied to this information to obtain levels of subsistence harvest for broad whitefish (broad

whitefish catch = $D \times C \times P \times H$). This method made use of locally obtained oral information so it is independent of the estimates produced by Treble (1996). However, the survey only reports harvest levels for the Inuvialuit Settlement Region. Estimated total harvest levels for the entire area must be adjusted to account for harvests in the Gwich'in and Sahtu Settlement Regions. Estimates using both methods are shown in Chapter Four.

Levels of adult natural mortality, juvenile natural mortality, and proportion of eggs successfully fertilized were estimated from literature sources discussing similar coregonid and other species (e.g., lake whitefish, *Coregonus clupeaformis*, and vendace, *Coregonus lavaretus* Salojarvi 1992a, d; vendace Fechem et al. 1995a, b; broad whitefish, Viljanen 1988; and lake whitefish and related salmonids Jensen 1981 brown trout, *Salmo trutta*).

Functional forms of equations describing processes were determined by finding functions in the literature that describe similar processes. The parameters associated with these functions and the particular form of the function was chosen using heuristic methods. For example, parameters were manipulated in a spread sheet format until the function produced values that were comparable to values in the literature. These functions were validated by comparing their use in other models as well as by using the technique of face validity. Then, once the function was fitted with suitable parameters an experimentation phase with the model began. The function and its parameters were then tuned in order for the model to yield sensible outputs that were determined by the estimation of adult population size (Delphi-Technique), and the estimation of the level of exploitation (Treble 1996 and Freeman 1997). Many of the parameters and functions of the model were derived without empirical data, so stochastic variables were used to produce variance around a mean value of a parameter (Table 2). Variance around a mean is necessary to

realistically simulate the dynamics of a natural system (Hagiwara and Mitsch 1994). Parameter values and functions that were estimated without any measure of variance are varied by assigning them a standard deviation, which attempts to produce a normal distribution that ranges approximately 20 % on either side of a mean. Hagiwara and Mitsch (1994) used this method of simulating the dynamics of a natural system in the absence of empirical information.

The production of a random number is essential to the production of a stochastic computer simulation model. A random number is a stochastic variable that meets certain conditions: 1) the variable is uniformly distributed over the interval from zero to one and 2) a sequence of these variables shows statistical independence (Kleijnen and Van Groenendaal 1992). The random number generator (RAN 1) was used to return a uniform random deviate between 0.0 and 1.0. The random number generator, RAN 1, is based on three linear congruential generators and a shuffler (Spratt 1991). The output from RAN 1 is transformed into a Gaussian deviate using the routine GASDEV (Spratt 1991). The routine, GASDEV, returns a normally distributed deviate with zero mean and unit variance. The seed values for each of these routines are changed each time before the routines are executed.

Non-standard normal distributions are simulated by transforming the standard normal distribution to a non-standard normal distribution. Using the normally distributed random number obtained from the routine GASDEV does this. This value is multiplied by the standard deviation chosen for the distribution in question. This product is then added to the mean of the distribution in question to yield a normally distributed random value for the parameter.

3.3.5 Formal Model Synthesis

The conceptual model which represents many of the important processes involved in the life-cycle of the Mackenzie River broad whitefish was validated by exposing the flow diagram to critical reviews by experts. During this process of face validity, the model's assumptions were assessed for legitimacy, the input parameters were assessed for their reasonableness as well as the reasonableness of the output. Also, where possible statistical validation was used, i.e. fecundity data in determining if they were significantly different than another source and validating the assumption that the data conformed to a normal distribution. After experts supported the conceptual model, the abstract model was converted into the actual computer model. The Visual Basic programming language used allowed me to construct a simplified version of the conceptual model first, then as the code was debugged and verified, the more complex processes could be added to the model in discrete components or modules one at a time. This process involved the production of several versions of the model until a complete and solvable version of the model was produced. This process of validation during this step can be termed trace analysis. -

3.3.6 Design and Execution of Experiments

Sensitivity analysis was carried out in two discrete steps. The first step was the calculation of the average elasticities of the parameters. The elasticity of the parameters used in the model was calculated as in Evans and Dempson (1986). The relative change in the output of the model as compared to the change in the value of the parameter is called the relative elasticity of that

parameter. All fourteen parameters (Table 5) in the model had their elasticities calculated in the following way. The model is set to run for 600 replications with the parameter in question being designated at a "low" value while all other parameter values are set to their normal values. Then the same procedure is conducted with the parameter in question now designated at its "high" value. Information from the literature as well as the ability of the model to function logically, defined the high and low values of the parameters in question. In the absence of empirical information describing particular parameters the most extreme values that were biologically reasonable and passed face validation that the model would accept and continue to function correctly were used. The mean values of population size for the replications are used in the equation:

$$Elasticity = \left[\frac{popsize(H) - popsize(L)}{Px(H) - Px(L)} \cdot \frac{Px(L)}{popsize(L)} \right] \quad (6)$$

where: $popsize(H)$ is the population size at the high value of the parameter,
 $popsize(L)$ is the population size at the low value of the parameter,
 $Px(H)$ is the high value of the parameter, and
 $Px(L)$ is the low value of the parameter.

Elasticities were calculated in order to determine which parameters would have the greatest effect on the abundance of the population in the conceptual system. The four most elastic parameters that were used in a factorial designed experiment (second stage of the sensitivity analysis) were not the most elastic. In fact the two parameters involved in the density dependent function governing the juvenile portion of the population were the most sensitive. However, these two parameters were omitted from further sensitivity testing due their extreme

TABLE 5. Parameter elasticities and their associated high and low range values. A description of parameter abbreviations is provided below.

Parameters	Elasticities of Parameters to Population Size		
	Elasticity	Parameter Levels	
		Low	High
P1	0.29	14,500	74,000
P2	0.06	0.8	1.2
P3	0.43	0.66	0.99
P4	0.26	0.1	0.5
P5	-0.75	0.5	0.9
P6	-0.02	0.01	0.2
P7	11.5	0.8	1.2
P8	-0.63	0.8	1.2
P9	-0.07	0.05	0.5
P10	-0.09	0.05	0.5
P11	-0.09	0.05	0.5
P12	-0.30	0.5	0.9
P13	-0.10	0.05	0.25
P14	-0.11	0.05	0.35

Description of Parameters

- P1: fecundity
- P2: number of successfully fertilized eggs
- P3: level of egg survivorship
- P4: percentage of larvae becoming trapped in delta lakes
- P5: mortality of larvae in delta lakes
- P6: daily larval mortality during downstream migration
- P7: juvenile density dependent parameter in tundra lakes
- P8: juvenile density dependent parameter in tundra lakes
- P9: coastal fishing mortality
- P10: delta fishing mortality
- P11: pre-spawning fishing mortality
- P12: ratio of upstream and downstream fishing mortality
- P13: post-spawning mortality
- P14: natural overwintering mortality

elastic responses (Table 5), that would have biased the results obtained from further sensitivity analysis. Also, our ability to gather in depth information regarding this process is unlikely, therefore any further analysis of this process at this time would be futile.

This next stage of sensitivity testing involves the quantification of parameter and interactive effects. Quantifying the effect of parameters and the interactions between parameters is an important process in formulating an adaptive management strategy. An adaptive management strategy will aim at reducing the uncertainty of the management decision by performing deliberate experiments to obtain information regarding stock recruitment dynamics (Hilden and Kaitala 1991). Also, testing the sensitivity of the model results to assumptions and input data can provide guidance on data collection and compilation procedures (Megrey and Wespestad 1989). The parameters to which the model is most sensitive are the ones most important to consider estimating using empirical information. This would involve the development of studies designed to gather specific empirical information. In an uncertain world, management actions aimed at altering such parameters are safer than other actions (Evans and Dempson 1986).

Analyzing these three parameters using an experimental design framework allowed me to quantify the effect of each parameter individually as well as the interactive effects between the parameters. A two-level full factorial design was used in this analysis (Box et al. 1978). Table 6 shows a 2⁴ factorial experiment in which there are four quantitative variables (egg survivability,

Table 6. Description of the 2⁴ design matrix involving P1, P3, P5, and p12. The effect sizes and the standard errors are shown for the four parameters and their interactions.

RUN	design matrix variables				estimated effect	standard error	identification
	P1	P3	P5	P12			
1	-	-	-	-	1528186	8339	average
2	+	-	-	-	1162649	9596	P1
3	-	+	-	-	105889	13281	P3
4	+	+	-	-	-3830	9920	P5
5	-	-	+	-	-1351423	17847	P(12)
6	+	-	+	-	-231027	6681	P1P3
7	-	+	+	-	-86499	8914	P1P5
8	+	+	+	-	7951	10463	P1P(12)
9	-	-	-	+	-549342	6623	P3P5
10	+	-	-	+	-45632	8311	P3P(12)
11	-	+	-	+	-152659	9249	P5P(12)
12	+	+	-	+	-3652	8682	P1P3P5
13	-	-	+	+	95438	11045	P1P3P(12)
14	+	-	+	+	166895	4656	P1P5P(12)
15	-	+	+	+	-54068	10648	P3P5P(12)
16	+	+	+	+	-22946	6899	P1P3P5P(12)

fecundity, mortality of juveniles in delta lakes, level of upstream and downstream fishing mortality). In this design each of the factors (variables) occur at only two levels (high and low). Therefore, sixteen experimental runs are needed (i.e. $2 \times 2 \times 2 \times 2 = 16$).

3.3.7 Evaluation of Results

Each experimental run or design was replicated 600 times and an average of the output for each replicate was used. The number of replications was determined by analyzing the variance of model output for different lengths of replications. The number of replications where the greatest decrease in variance was noted was chosen as the most efficient number of replications to be used in the analysis of the model output. Replication lengths ranging from 100 to 1000 were analyzed at intervals of 100. A dramatic drop in the variance associated with model runs was noticed for replications around a magnitude of 600 (Figure 16).

The length of time the model requires to reach a steady state is termed the transient phase (Law and Kelton 1991). Results produced during the transient phase must be removed from the data used in the analysis to avoid biasing the results (initialization bias) (Power and Power 1994). A 150-year time interval was chosen because this time frame allowed the model to achieve a steady state under a wide range of input parameters within 50 years. The end of the transitory phase was estimated visually to end within 50 years. Using the technique of replication-deletion the estimate was validated. The transitory phase (the initial 50 years) of the model output was then removed from further

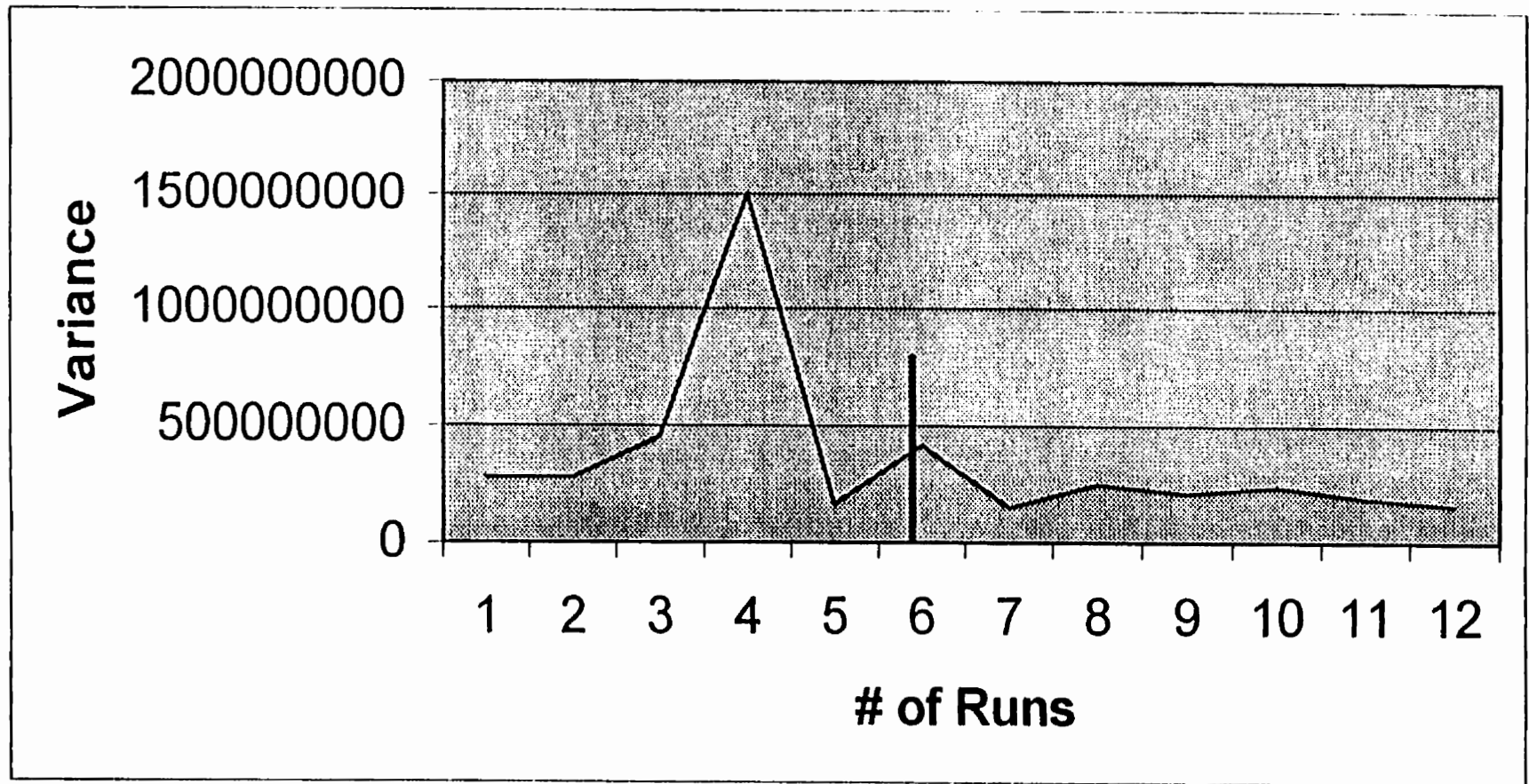


Figure 16. Diagram showing the variance associated with different numbers of replications in intervals of 10. Results indicate that the variance associated with model output replicated 500 or more times remains similar. Therefore, the vertical line indicates the number of replications chosen to use during all experimentation with the model.

analysis. This removed initialization bias in comparisons of model output between different experiments. This allowed the remaining 100 years to be used for analysis. The time period of 100 years should be adequate for analysis because it would allow the model to generate more than ten generations of fish per run. The response (output) was the size of the adult population.

Experimentation with the model provided insight into the conceptual systems behaviour. The effects of parameter sensitivities, parameter interactions, and fishing pressure were explored. A descriptive presentation of these experiments and the determination of how the model is best used will be given in Chapter Four. Inferences about the system made from the collection of model outputs will be discussed in Chapter Five.

3.4 Model Description

Processes involved in the life cycle of the broad whitefish are shown in the conceptual model shown in Figure 13. The model depicts most of the major events that a broad whitefish will encounter throughout its lifetime. The model does not incorporate age structure into the population except for the juvenile phase of the life cycle (age zero through eight). A general assumption in fishery science today is that age best accounts for variation in vital population parameters (Caswell et al. 1984). However, survival and reproductive success are often size-related, rather than being pure functions of age (Caswell et al. 1984). The use of a life-cycle model for anadromous coregonids that uses life stages instead of age classes was shown by Morin and Doidge (1992). They showed that a stage-based model can adequately describe a population with many age classes. Stage-based models have an advantage in their application to anadromous coregonid dynamics (Morin and Doidge 1992). This type of

approach is adaptable to organisms with complex life cycles but this type of model requires comprehensive knowledge of the life cycle in order to collect relevant data regarding important parameters. The model is primarily a stage based model because the life cycle is described by a series of life stages rather than annual age increments (Morin and Doidge 1992). However, the juvenile component of the model uses age classes to keep track of maturing juveniles as they enter the fishery.

The following paragraphs provide a step by step explanation of each process and function described in the conceptual model and used in the computer model, (See Figure 13).

It is thought that the Mackenzie River broad whitefish have a two-year cycle of reproduction and a sex ratio of 1:1 (Reist and Bond 1988, Tallman and Treble 1997). With this in mind, I calculated the number of spawning females in any given year by dividing the total number of adults by two to get the number of females in the population. Then the numbers of females were divided by two to determine the number of females spawning in a particular year. Therefore, one-half of the population is composed of females and one-half of these females are assumed to spawn during any one year. The remaining females are assumed to be resting in that particular year.

The mean value of fecundity is varied stochastically using a normal distribution with a mean value of 44, 257 with a standard deviation of 14, 840. The number of eggs deposited on the spawning grounds each year is calculated by multiplying the number of spawning females in any one year by the given value of fecundity.

A Beverton-Holt (B-H) curve is assumed to best represent the effects of egg mortality due to limitations in suitable spawning habitat (Hilborn and Walters 1991). This function is a logical choice over a Ricker-type function because of

the spawning behaviour of the broad whitefish. Unlike salmon, it is assumed that broad whitefish are not severely limited in suitable spawning habitat and do not exhibit territoriality nor dig redds (personal communication Ken Chang-Kue). However, a simple linear relationship does not represent egg mortality well either. Thus, it was assumed that a finite amount of eggs could be successfully reared on the spawning grounds. Population sizes on the spawning grounds above the high levels obtained from the Delphi-Technique (Table 7) will fail to increase the amount of offspring produced due to cannibalism, laying eggs in unsuitable areas, egg suffocation by being packed too tightly, or the failure to lay eggs. Therefore the B-H function used in the model is of the form:

$$\text{Surviving Eggs} = \frac{aS}{1 + (a/b) \bullet S} \quad (7)$$

where: S is the number of spawning females,
 a is the maximum number of recruits that could be produced, and,
 b is the number of spawning females needed to produce recruitment equal to a/2.

At low to moderate population sizes (one to five million) calculated egg mortality remains low at 10% or less. However, at extremely high population sizes (> 10 million), egg mortality calculated from the model begins to increase. Experts accepted the B-H function during various intervals of face validation. This function was regarded as a suitable model to describe the processes on the spawning grounds because the production of young is usually not so great that crowding, egg suffocation, or cannibalism are important factors. However, at

Table 7. Calculated statistics showing the Minimal, Median and Maximal estimates obtained from the 8 experts surveyed in the Delphi-Technique Questionnaire.

Minimal		Median		Maximal	
Mean	1044791.63	Mean	3390625	Mean	7315625
Median	600000	Median	1500000	Median	3200000
Mode	600000	Mode	10000000	Mode	20000000
S. D.	1067307.53	S. D.	4143883.99374	S. D.	8455629.33262
Variance	1.1391E+12	Variance	1.717177E+13	Variance	7.149767E+13
Minimum	325000	Minimum	375000	Minimum	425000
Maximum	3333333	Maximum	10000000	Maximum	20000000

extremely high population densities these conditions may exist and increase egg mortality (Elliott 1990a).

The number of viable eggs produced is assumed to be governed by this density-dependent process which can be modeled by the Beverton-Holt equation, i.e., equation 7 above (Beverton and Holt 1954). This function yields the number of eggs that will have a chance to hatch. A proportion of these eggs will hatch. The precise proportion of eggs hatching is determined by randomly obtaining a percentage from a normal distribution with a mean value of 90 % and a standard deviation of 3%. This mean value was obtained by Bogdanov et al. (1991) who estimated the percentage of broad whitefish eggs that successfully hatch. After this function is executed, the number of larvae produced for that particular year have been calculated.

In the model the larvae that are produced on the spawning grounds may successfully reach their rearing grounds on the Tuktoyaktuk Peninsula during the first summer. However, larvae that are unsuccessful at reaching the lakes on the Tuktoyaktuk Peninsula can suffer a variety of fates: 1) they can become trapped in delta lakes and die over the winter; 2) they can become trapped in these delta lakes, survive over the winter and rejoin the anadromous population during the next spring (provided water levels are high enough), at an age of 1 +; or, 3) they can reside in these lakes for an unknown period of time and perhaps even reproduce there (Reist and Bond 1988). In the model only two options are available to the larvae - reaching the Tuktoyaktuk Peninsula or trapped in Delta lakes. From qualitative descriptions in the literature made by, (Bond and

Erickson 1987, Reist and Bond 1988, Chang-Kue and Jessop 1992), all of which indicate that the majority of juveniles get swept into the Beaufort sea where they find their way into the shallow lakes on the Tuktoyaktuk Peninsula while the other remaining juveniles end up tundra lakes within the delta. Therefore, it was assumed that 80 % of the larvae that hatch will reach the tundra lakes and the remaining 20% of larvae will become trapped in lakes within the delta. During the downstream migration of the larvae (Module Two), the model splits the larvae into two groups that have two different fates. One group of larvae (20 %) will lag behind the other group in migrating downstream by one year. This smaller proportion represents individuals that become trapped in the delta lakes during high spring flood waters, survive over winter, and re-enter the juvenile population one year later. The larger group of larvae (80 %) will continue to migrate downstream and enter their rearing grounds (small freshwater lakes on the Tuktoyaktuk Peninsula and Richard's Island). Consequently in Modules Three and Four the two groups of larvae experience levels of mortality unique to each group.

It was assumed that of the 20 % in the delta lakes, 80 % of these larvae will suffer overwintering mortality. The high mortality experienced by this group of larvae is due to overwintering habitat shortages (these lakes are shallow and many freeze to the bottom during winter) and predation (northern pike, burbot) in the delta lakes. Taylor et al. (1982) found that pike consumed four, ten, and fifty times the fish biomass that migrated through their weirs in the main channel from three delta lakes. Larval survival in the delta lakes is likely to be severely

decreased relative to that in the lakes on the Tuktoyaktuk Peninsula due to the lower levels of predation.

The majority of the larvae (80 %) migrate downstream to the Tuktoyaktuk Peninsula (Reist and Bond 1988). The larvae that are produced in the upper reaches of the mainstem of the Mackenzie River and tributary rivers such as the Arctic Red River and the Peel River take approximately sixty days to reach the outer delta area (Bond and Erickson 1985, Chang-Kue and Jessop 1992). Bogdanov et al. (1991) noted variable mortality (0 % to 10 %) during the descent downstream due to the chance of encountering predators or catastrophic events such as ice jams. This form of density-independent mortality is modeled by randomly choosing levels of total downstream mortality from 0 % to 10 % from a normal distribution with a mean value of 5%.

Juveniles in the lakes on the Tuktoyaktuk Peninsula and Richard's Island are assumed to suffer density-dependent mortality. The model causes the severity of this mortality to decrease as the fish age (Ricker 1975, Rotschild 1986). This model represents these density-dependent effects through the equation of the form, $(S = Ke^{-md} + (1 - K))$. (8) -

Where: S is the % of juveniles from $t(i) + 1$
K is the amount of natural mortality (density independent) experienced by that year class
M is density dependent parameter, and
d is the number of juveniles in $t(i)$

This relationship models the rate of mortality as a function of year-class size during the first year of the fish's life. However, fish could rear in the lakes for

eight more years. It was assumed that as a fish becomes older they are less vulnerable to density-dependent effects and the rate of mortality will decline with age. Johnson (1972, 1976) believed that larger, older lake whitefish suppress younger, smaller individuals and that as the older, larger fish died or in this case leave the lakes an equal number of recruits were allowed into the stock.

Therefore, smaller subordinate individuals would be forced into unfavourable habitat or otherwise behaviourally suppressed by the larger individuals. It is assumed that this process also occurs in the lakes used for rearing juvenile broad whitefish. The relationship between age and density-dependent juvenile mortality from ages one through to first sexual maturity can be represented by decreasing the magnitude of the curve produced by the above equation on a yearly basis.

Each age of the juveniles from age one to five had a different form of the above equation. Age one fish experienced a higher degree of density-dependent mortality than fish of age five. The five different forms of the equation above represented a decreasing amount of density-dependent mortality from ages 0+ through 5+. After the age of five and through to the age of eight, it was assumed that the effects of density-dependent mortality give way to constant proportional mortality. After the age of five most broad whitefish will have survived to the end of their "critical period". After this period density-dependent processes no longer play as large a role in population regulation; the most significant effects are again realized through density-independent processes.

The set of equations used to generate the relationship shown in equation 8 calculates the number of mature individuals that leave the lakes on the Tuktoyaktuk Peninsula and join the adult population. The number of fish that reach the age of eight were assumed to be sexually mature and therefore migrate to the spawning grounds in that year (Bond and Erickson 1985, Chang-Kue and Jessop 1992).

Sexually mature fish leaving the rearing grounds (tundra lakes) are exploited at coastal areas such as Tuktoyaktuk Harbor, Whitefish Station, and Shingle Point (Figure 6). Regardless of which stock these migrants belong to they were thought to be exposed to the same level of exploitation at this point in the model because all fish leaving the rearing grounds pass by the same areas of exploitation. The total catch at these locations mainly equals the number of first time spawning individuals that were intercepted on their way to the spawning grounds. The amount of fish caught at this point in the model was represented by the variable C1. The fish that escape exploitation (MatVE) move south to mix with the existing mature component of the population in the inner delta. In Module Six this exploitation was represented by the equations below:

$$C1 = MatV * F1 \quad (9a)$$

$$MatVE = MatV - C1 \quad (9b)$$

where: F1 is the level of total exploitation assumed in coastal areas,
C1 is the number of first-time spawners caught,
MatV is the number of mature first-time spawners leaving tundra lakes, and,
MatVE is the number of mature first time spawners escaping coastal fishing mortality.

Fish escaping exploitation mixed with the overwintering portion of the population in the inner delta.

The overwintering portion of the population was a mixture of mature individuals from all four stocks. All individuals of this overwintering portion of the population that were in spawning condition begin their migration southward to their spawning grounds in late summer.

The probability that a fish migrated was assumed to be linked to its energy reserves. Therefore, if a fish did not migrate the previous year and also did not spawn thus avoiding such energetic demands, it would have had a high probability of migrating the following year. Conversely, if a fish migrated a large distance the previous year and was faced with the great energetic demands associated with spawning, it would have had a low probability of migrating the following year. Evidence for this was provided by Reist and Bond (1988), and Chang-Kue and Jessop (1992). I assumed that 50 % of the adult population would remain in the outer delta to overwinter and store energy reserves in order to take part in the migration the following year. The remaining 50 % was assumed to be the migrating group which moves southward towards Horseshoe Bend. Here, these fish likely congregate in the slow moving waters in this eddy from late August to early October, before exhibiting a concerted run upstream to their spawning grounds. The amount of time spent in this area is important because this area is the focus of much subsistence fishing effort, subsistence and potentially commercial exploitation also. At this time, during their upstream migration, it was assumed that 100% of the annual total catch for this area was obtained because the fishery intercepts upstream migrants only. The total catch at this point in time must include catch from the commercial fishery at Horseshoe Bend, and subsistence catches from areas located throughout the delta area,

Inuvik, and Aklavik. Module Seven represents the exploitation that occurs in this area by the equations:

$$C2 = MataS * F2 \quad (10a)$$

$$MataSE1 = MataS - C2 \quad (10b)$$

where: F2 is the level of total exploitation assumed in the delta area,
C2 is the number of mature adult spawners caught in the delta area,
MataS is the number of mature adult spawners migrating through the delta area, and,
MataSE1 is the number of mature adult spawners escaping fishing mortality.

Fish managing to escape this fishery (MataSE1) continue to migrate up river where they are again met by interception fisheries at the locations of Tsiigehtchic, Fort McPherson, and Fort Good Hope. It is assumed that the catch from these areas was composed of 70 % upstream migrants (pre - spawners) and conversely 30 % of downstream migrants (post - spawners). This is an important assumption because most fish will be exploited before spawning. Also, the exploitation rate of pre-spawners versus post-spawners should be split into 70 % upstream, (pre-spawners) and 30 % downstream migrants (post-spawners) for the following reasons: 1) The upstream migration of broad whitefish is much more concentrated in time and space than in the downstream migration. This causes the catchability to increase; 2) The upstream migrants move along the edge of the river or follow areas of least resistance, and maintain tighter schools in order to conserve energy. By doing so they are more susceptible to fishing gear; 3) Conversely, the downstream migrants are able to ride the current downstream in the middle of the channel where the flow is the fastest. This causes the catchability to decrease because fishing gear is generally not employed in these areas; 4) Effort drops off considerably by this

time of the year due to inclement weather conditions and increasing ice thickness. This sensitivity of the level of upstream and downstream fishing mortality was formally tested.

Since the model represents the different stocks as one uniform stock, exploitation from the above areas was summarized into one value (pre-spawning exploitation) in Module Eight. This was represented by the equation below:

$$C3 = MataSE1 * (F3 * 0.70) \quad (11a)$$

$$MataSE2 = MataSE1 - C3 \quad (11b)$$

where: F3 is the level of combined total exploitation at the communities of Fort McPherson, Tsiigehtchic and Fort Good Hope,
C3 is the number of adult migrants (MataSE1) caught at the above locations,
and,
MataSE2 is the number of adult migrants (MataSE1) reaching spawning grounds.

Fish escaping this source of exploitation reach the spawning grounds and successfully reproduce.

After spawning, individuals were assumed to suffer post - spawning mortality at a mean level of 5%. This level of post-spawning mortality is reasonable because Tallman (unpublished data) observed that the numbers of broad whitefish during the upstream – pre spawning migration was nearly equal to the downstream – post spawning migration. This information indicates that a very low level of post spawning mortality occurs. This value for post spawning mortality was also subjected to face validity. For mature fish natural instantaneous mortality (M) must be low because they have many age classes. The value of M at 0.2 is used on the east coast for cod which have roughly the same number of age classes. This value takes into account post-spawning mortality as well. Since overwintering mortality for broad whitefish has been set

to equal 0.2 the value for post-spawning mortality must be set very low to balance the longevity of the species. This is the only significant source of natural mortality that migrating fish incur because during events of fishing mortality natural mortality can be assumed to be negligible (Hilborn and Walters 1991). The parameter value for this parameter is chosen stochastically during each time step from a normal distribution between one and nine percent. This mortality is due to general physical debilitation resulting from spawning, i.e., the high expenditures of energy needed for the lengthy migration (350 km) and the production of gonads.

Spent individuals of each of the four spawning stocks pass through all the same fisheries as they did during their migration upstream, with the exception of the commercial fishery at Horseshoe Bend, and the fisheries at Tuktoyaktuk Harbour, and Whitefish Station. However, as illustrated by the 70/30 split in catch of pre-spawners to post-spawners, post-spawning individuals were subjected to a substantially lower rate of exploitation. As stated before, 30% of the total catch in these areas was made up of post-spawning individuals. The remaining 30% of the exploitation that occurs at the pre-spawning areas was focused on the fish that survive reproduction and begin to migrate downstream. This function is shown by the equation below:

$$C4 = MataPS * (F3^l * 0.30) \quad (12a)$$

$$MataPSE = MataPS - C4 \quad (12b)$$

where:

F3 is the level of combined total exploitation at the communities of Fort McPherson, Tsiigehtchic and Fort Good Hope,

C4 is the number of adult migrants (MataSE1) caught at the above locations,

MataPS is the number of post spawning fish to pass through areas of exploitation, and,

MataPSE is the number of adult migrants (MataSE1) reaching spawning grounds.

The above two sources of mortality (post-spawning natural mortality and post spawning exploitation) occur consecutively in Module Ten.

Spawners escaping post-spawning exploitation reach the outer delta and mix with the over-wintering portion of the population (resting fish). The fish that did not take part in the migration were assumed to experience a mean over-wintering mortality level of 20 % which is an acceptable level for natural mortality of long-lived fishes (Healey 1975, Howe and Coates 1975, Thompson and Davies 1976, Schneider et al. 1977). The resting portion of the population feeds in the outer delta and the following year fish that have acquired enough energy (50 % of the adult population) will migrate to the spawning grounds. This relationship occurs in Module Eleven. The remaining Modules Twelve, Thirteen and Fourteen contain routines for the random number generator (RAN 1 and GASDEV), and for handling output from the model.

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 Analysis of Sensitivity

Output can be analyzed in terms of its sensitivity to assumptions and changes in parameter values. Testing the sensitivity of model results to assumptions and input data can provide guidance on data collection and compilation procedures (Megrey and Wespestad 1989). Whether a model is used to reflect understanding or to predict the effects of management actions, it is important to know the sensitivity of the model outputs to the input parameters (Evans and Dempson 1986). In the beginning of a simulation study there may be many factors that are potentially important; unfortunately, we cannot readily identify which factors are unimportant from those that are really important (Kleijnen and Van Groenendaal 1992). If there is a large number of factors then classical techniques such as experimental designs will require too many combinations and therefore too much computer time. A method called screening provides a solution to this problem.

4.1.1 Parameter Elasticities

To screen the fourteen parameters (described in Table 2) in order to obtain insight into the more sensitive parameters of the model, their relative elasticities were calculated. Parameters having the greatest affect in the model were identified by observing the calculated elasticity for each parameter and noting the relative magnitude of departure from zero. The greater the result departed from zero the more elastic (sensitive) was the parameter (Table 5,

Figure 17). Of the 14 parameters in the model, six parameters were determined to have significant influence on model output. The parameters P1 (fecundity), P3 (egg survivability), P5 (larval mortality in delta lakes), P7 (juvenile density dependent parameter), P8 (juvenile density dependent parameter), and P12 (ratio of upstream and downstream fishing mortality) were calculated as the most sensitive.

Two parameters (P7 and P8) had elasticities that were an order of magnitude greater than elasticities for the remaining four parameters. The model was highly sensitive to these two parameters that dealt with the density dependent effects assumed to be associated with the juveniles in the fresh water lakes on the Tuktoyaktuk Peninsula. Any interactive effects between the six parameters would be overshadowed by the extremely high interactive effects associated with parameters P7 and P8 and the ability to collect useful information regarding these parameters was questionable, therefore they were omitted from further analysis.

However, six important parameters were identified using this screening process. The screening process is useful because the goal of experimental design theory is to gain insight into the system's behaviour while observing relatively few factor combinations (Kleijnen and Van Groenendaal 1992). Four of the six sensitive parameters were analyzed further using a 2⁴ full factorial design methodology.

Percent change from F=0 at Coastal, Delta, Pre-Spawning and all locations combined.

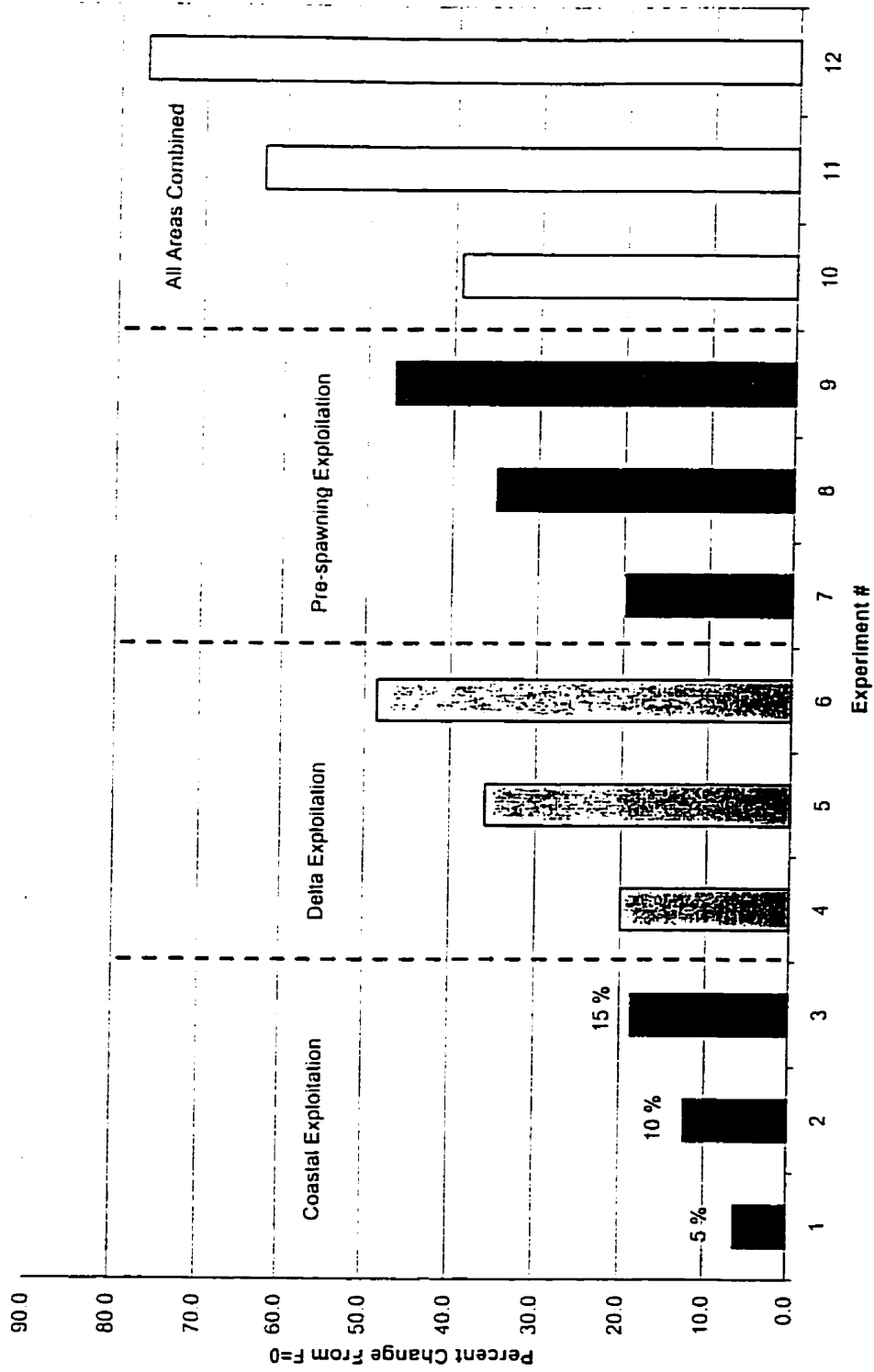


Figure 17. The percent change in the mean adult population size when comparing model output under 0% fishing mortality levels to 5%, 10%, and 15% fishing mortality levels at each location (coastal, delta, and pre-spawning) and all locations combined.

The high and low values of each of the parameters were primarily obtained by heuristic methods. In the cases where no quantitative data could be found the greatest difference (+\-) from the estimated mean value that would allow the model to operate correctly was used. Extreme high and low values which remained biologically reasonable and were subjected to face validity were used in preliminary tests with the model. If the estimated extreme values yielded biologically reasonable results and were comparable to other models and systems they were accepted as a high and low value for the parameter in question (Table 5).

4.1.2 Experimental Design

Table 5 shows all fourteen parameters, their extreme high and low values used to calculate their elasticities. From the table, six parameters are noted as being significantly elastic. However, due to reasons mentioned previously, P7 and P8 were excluded from further sensitivity tests.

Sensitivities and their interactive effects for parameters P1, P3, P5 and P12 were quantified using an experimental design (2^4 full factorial design). The design matrix was outlined using actual units of variables and using coded units of variables in Table 6. Main and interactive effects along with their standard errors are also displayed in Table 6.

The parameter describing fecundity (P1) had the greatest effect in the conceptual system. The parameter describing the ratio of upstream and downstream fishing mortality (P12) had the second greatest on the conceptual system. The interactive effect between the parameter describing egg

survivorship (P3) and the parameter describing the level of mortality larvae will experience in the delta lakes (P5) appears to be the next most significant effect in the conceptual system. The two factor interactive effect between P1 and P3 (P1xP3) is the next most significant effect in the conceptual system. All other main and interactive effects appear to be less significant.

In summary, results indicated that six parameters were of importance in the model that emulates the life cycle and population dynamics of the broad whitefish in the lower Mackenzie River. However, parameters P7 and P8, the parameters regulating the intensity of juvenile density-dependent mortality had the greatest effect on the conceptual system. This result was not surprising because population regulation mechanisms act primarily on the juvenile stages of the life cycle. Because density-dependent mortality was assumed to occur and the parameter "m" was estimated from next to no empirical information the predictive ability of the model was severely restricted. Due to the extreme sensitivity of the model to these parameters and the poor chance of collecting data in order to accurately describe these parameters, these two parameters were excluded from the experimental design framework.

4.2 Experimentation with the Model

The effects of exploitation on the conceptual system were explored by comparing the changes in adult population size between various levels of fishing mortality. Exploitation was divided into three different areas (Coastal, Delta, and Pre-spawning). Simulations where fishing mortality was set to zero were

compared to independent simulations where fishing mortality was set at a mean value of 5% at each of the three different locations (Table 8). Using a t - test with an alpha of 0.05, significant differences in population sizes were observed when model output for 0% fishing mortality (run 1) was compared to model output when fishing mortality was set to a mean value of 5% the coastal location (run 2). The mean population size decreased by a much greater extent when 5%, 10%, and 15% fishing mortality rates were applied at each of the other areas (delta and pre-spawning areas), (Table 8). Therefore, no further t - tests were used to establish the significance between the different mean values of population size under different scenarios of fishing mortality.

The percent change in the population size from the system operating under 0% exploitation is shown in Figure 17. In each of the four experiments (coastal, delta, and pre-spawning locations as well as all areas combined) exploitation levels were varied between 5%, 10%, and 15%. The percent change in the population size is shown. Exploitation in the delta and pre-spawning areas appears to have the most significant impact on the population size.

A cumulative percent frequency histogram of the resulting adult population sizes after 600 replications of the model with exploitation levels set at 15 %, 10 % and 25 % for the coastal, delta and pre-spawning areas respectively is shown in Figure 18. All other parameters in the model were varied normally around their mean values. The plot is a good representation of the resulting population sizes that may arise under fishing mortalities that may have been indicative of exploitation rates that occurred in the 1950's (Treble 1996a).

Table 8. Model experimentation analyzing different levels of fishing mortality (0%, 5%, 10%, and 15%) at coastal, delta, and pre-spawning locations. t-test indicates that there is a significant difference between mean adult population sizes at fishing mortality rates of 0% and 5% at each of the locations.

Experiment	Run #	coastal	delta	spawning	Mean Adult	
					Population Size	Standard Deviation
Experiment 1	1	0	0	0	8846962	49388
	2	5	0	0	8297255	49669
	3	10	0	0	7747291	49954
	4	15	0	0	7197113	50182
Experiment 2	5	0	5	0	7072142	38147
	6	0	10	0	5672904	31528
	7	0	15	0	4546654	26455
Experiment 3	8	0	0	5	7102694	37708
	9	0	0	10	5761173	30930
	10	0	0	15	4702763	26091
Experiment 4	11	5	5	5	5374360	31188
	12	10	10	10	3301228	19706
	13	15	15	15	2046152	9083

	<i>run 1</i>	<i>run 2</i>
Mean	8846963	8297256
Variance	2.4E+09	2.47E+09
Observations	100	100
Pooled Variance	2.5E+09	
Hypothesized Mean Difference	0	
df	198	
t Stat	78.4794	
P(T<=t) one-tail	2E-151	
t Critical one-tail	1.65259	
P(T<=t) two-tail	4E-151	
t Critical two-tail	1.97202	

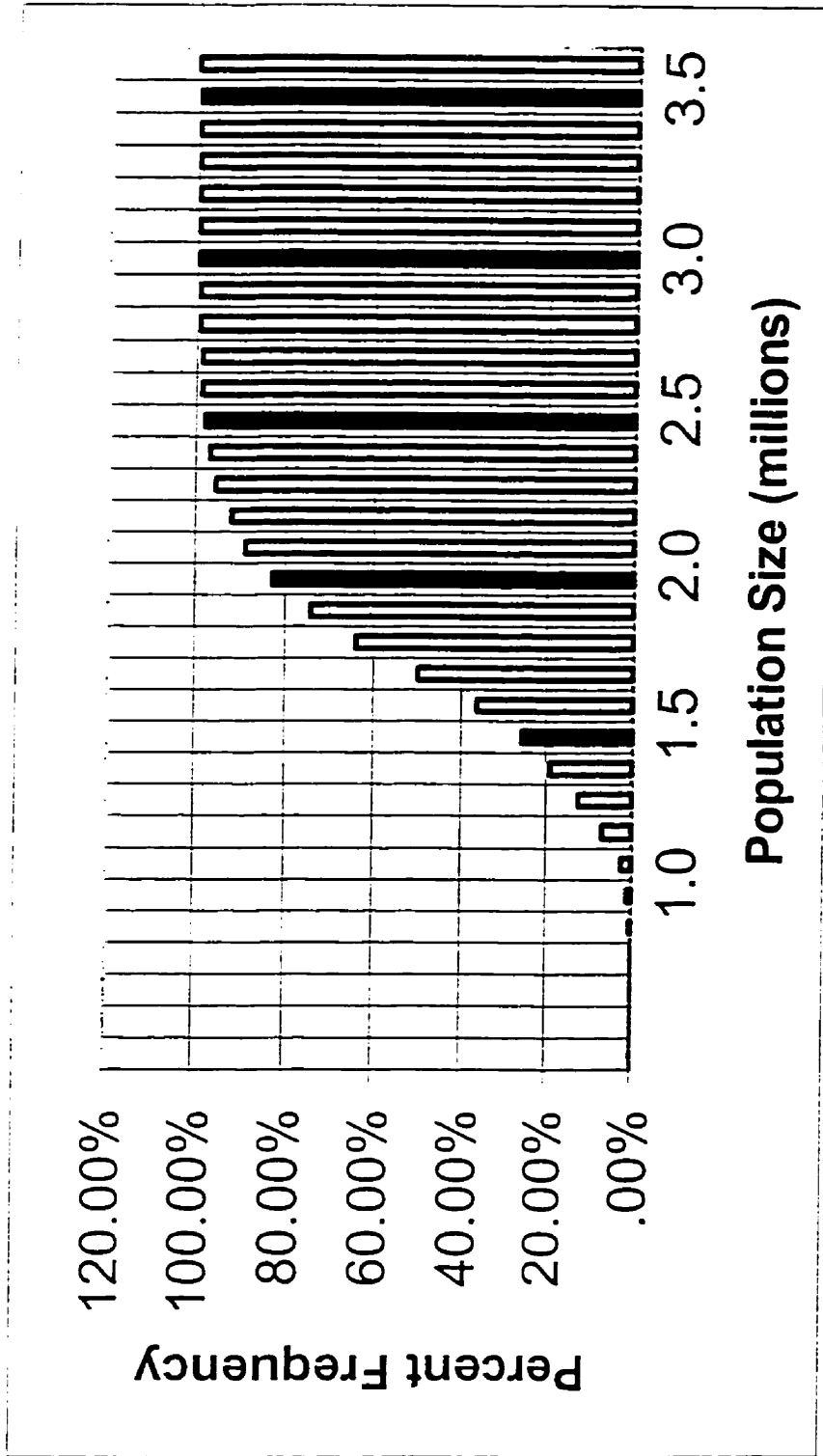


Figure 18. Percent frequency histogram of model output for the population size of adult broad whitefish under mean input parameter values. Fishing mortality was set to 15 % at coastal, 10 % at delta, and 25 % at pre-spawning locations.

Catch Curves for Broad Whitefish from the Inuvik Exploratory Fishery (1990-1993).

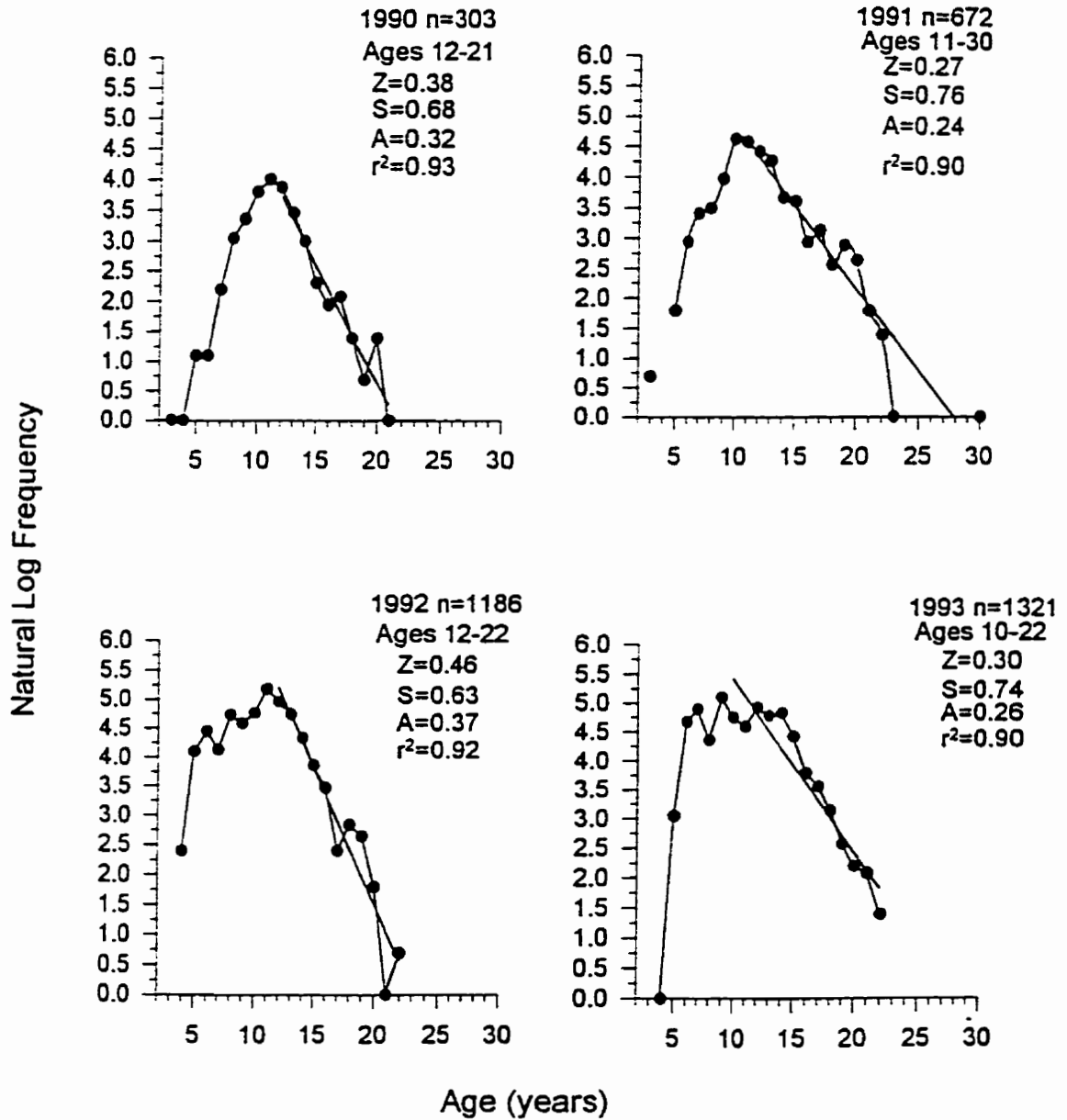


Figure 19. Age frequency catch curves for broad whitefish from the Inuvik exploratory fishery, 5.5" gillnets, 1990-1993. Instantaneous mortality (Z), survival (S), and annual mortality (A), have been calculated from the regression line for the descending limb of each curve (From Treble and Tallman 1997)

From this plot we can conclude that over 80 % of the time the population will stabilize at levels in excess of two million adult fish. Also, adult population sizes appear to be bound between approximately one and 3.5 million fish 100 % of the time with the exploitation levels set as noted above.

Historic levels of harvest are shown in Figure 15. The Exploitation rate (F) for the delta fishery was estimated to be approximately 0.16 (Treble and Tallman 1997). Catch curves produced from the exploratory commercial fishery (1989 - 1993), (Treble and Tallman 1997) provided the necessary data for estimating fishing mortality (Figure 19). Rates of fishing mortality (F) for coastal and pre-spawning areas were 0.1 and 0.25 respectively. Fishing mortality at coastal locations was assumed to be lower than estimates for the delta because of a lower amount of effort, and because the geography results in a lower level of catchability because fish are less confined to narrow corridors as in other parts of the system. Fishing mortality at pre-spawning locations was assumed to be higher than estimates for the delta because there was a higher level of effort in this area and fish are confined to narrow corridors (higher catchability due to "bottle neck" effect), i.e., the concentration of fish in space and time.

Estimated levels of catch were validated against catch estimates obtained from surveys by Lutra and Associates (1989), Sparling and Sparling (1988), and the Inuvialuit Harvest Study (Fabijan 1991) in addition to the Traditional Knowledge Study which only included harvests within the Inuvialuit Settlement Region (Freeman 1996). Freeman's study estimated annual harvest levels to be between 100,000 and 411,000 fish with midpoint values of 287,500 fish in the

early 1950's. However, over time exploitation may have decreased due to changes in culture and technology (Figure 9) combined with a decreasing population of broad whitefish (Treble 1996). Harvests may have fallen in recent years to levels around (50, 000 - 150, 000) fish per year. However, human population levels are returning to higher levels and people in the north are experiencing an increased awareness of living off the land which may maintain high harvest levels. Estimates of harvest levels at pre-spawning locations were not made because past studies were only concerned with Inuvialuit harvest, and pre-spawning areas of exploitation are also located in the Gwich'in land claim area. Therefore, if the traditional knowledge estimates of maximum harvest levels (Freeman 1996) are extrapolated to account for the entire lower Mackenzie River region by increasing the estimates three fold in order to account for all three land claim areas, harvest levels may reach one million fish per year. Rates of exploitation were also determined using heuristic methods to check the validity of rates estimated by the above two processes.

Using results produced by the model as grounds for speculation it is proposed that if fishing mortality levels (F) of 0.15, 0.10 and 0.25 are implemented at coastal, delta and pre-spawning locations respectively, then yields will reach levels of 685,691 (s.d. = 176974) broad whitefish at a stable adult population size of 1,706,398 (s.d. = 286,084), (Table 9). This level of effort likely does not exist today but may have existed in the early 1950's when exploitation was probably at its highest levels. The model indicated that if lower fishing mortality levels (F), of 0.05, 0.01, and 0.05 were implemented at coastal, delta,

and pre-spawning locations respectively, then approximately 357,279 (s.d. = 78,653) broad whitefish per year should be caught at a stable adult population size of 6,550,099 (s.d. = 1,051,002), (Table 9). Simulations of fishing mortalities (F) of 0.01 at all locations yield catches of 129,888 (s.d. = 22,978) broad whitefish per year at a stable adult population size of 8,402,049 (s.d. = 1,041,819), (Table 9). The last two simulations using lower fishing mortality levels produce yields that are presumably much closer to today's estimated catch levels. Simulated levels of catch as indicated above were initialized with a population size of five million.

Adult natural mortality is assumed to be negligible during the spawning migration because significant fishing mortality persists throughout the entire upstream migration (Hilborn and Walters 1991). Five percent mortality in the form of post-spawning mortality was assumed to occur immediately after spawning. Adult broad whitefish that remain in the outer delta to overwinter and do not take part in the spawning migration in addition to migrating fish are assumed to suffer 20 % overwintering mortality each year. This value of overwintering mortality was obtained from coregonid populations in the Sagavaniriktok River (Schmidt 1989). This level of natural mortality is commonly accepted as an estimate for natural mortality for a wide variety of long-lived species and therefore was used in this study (Healey 1975, Howe and Coates 1975, Thompson and Davies 1976, Schneider et al. 1977).

Table 9. Model experimentation showing expected mean population sizes and total harvest levels with their respective standard deviations in three different scenarios of fishing mortality.

Experiment	Fishing mortality levels		Adult Population Size	Total Annual Harvest
scenario 1	0.15, 0.10, 0.25	mean	1706398	685691
		S. D.	286084	176974
scenario 2	0.05, 0.01, 0.05	mean	6550099	357279
		S.D.	1051002	78653
scenario 3	0.01 at all locations	mean	8402049	129888
		S.D.	1041819	22978

An estimate of the adult population size was necessary to tune or confine many parameters within logical ranges as well as to determine a starting population size for the simulations. The Delphi -Technique proved to be an invaluable tool for estimating a crude population size or range of logical population sizes (Zuboy 1981), (Table 7). The average adult population size is estimated to be no greater than 7, 315, 625, with a range between one and twenty million (Table 7). A population size slightly lower than the estimated average was chosen to initialize all simulations in order to be conservative. The initial population size of five million was the value that parameters were tuned to under normal or steady state conditions. This value is reasonable because it was validated through discussion with experts (face validity). Preliminary model testing or stress testing provided confidence in the initial population size value used because the model produced logical values for catch at many harvest rates and maintained an adult population size within the range given in the Delphi-Technique survey throughout the model's operation.

CHAPTER FIVE

CONCLUSIONS AND FUTURE RESEARCH

5.1 SUMMARY

In order to aid in research planning, this study identified six parameters that have a significant effect on the output of the model describing the conceptual system. These six parameters were P1 (fecundity), P3 (level of egg survivorship), P5 (mortality level of larvae in delta lakes), P7 and P8 (both are juvenile density dependent parameters), and P12 (ratio of upstream and downstream fishing mortality). In the screening process, parameters governing the juvenile density dependent relationship were observed to be extremely sensitive. Thus, even slight changes in these parameters would have led to significant changes in the behaviour of the model. Because of the extreme sensitivities of these parameters and the low level of confidence associated with their estimation as well as the low probability of collecting data that accurately describes this phenomenon, these parameters were excluded from further analysis. If these parameters were to be included in further analysis, relevant information about roles other parameters play in the system may be obscured. Model behaviour such as: 1) a longer runtime required to achieve population stability, 2) different numbers of estimated adults at stability with even slight changes in parameter values, 3) Important interactive effects between parameters may be overshadowed by the powerful effects of the extremely sensitive parameters.

Validation is a critical exercise in systems analysis and simulation experiments (Power and Power 1994). Van Horn (1971) defined validation as any process designed to assess the correspondence between the model and the system studied. Although validation is an ongoing process throughout the development and construction of this model validation can be described as occurring in three major phases: 1) Data validity which involves evaluating the data used in the model for accuracy and representativeness. Validity of the model was enhanced wherever possible by including data from the study system. Where data from the actual system or similar systems could not be obtained theory was used to establish, a priori, the nature and form of data inputs. Empirical tests like t-tests, distributional tests, goodness of fit tests established confidence in the data used in the model. 2) Conceptual model validation is another phase of validation that focused on determining if the overall model and sub-models and the theories and assumptions used to construct them are correct. This involved trace analysis of the pseudo-code and logic of the model as well as face validation of the assumptions, and pseudo-code by selected experts. Verification, the process of comparing the conceptual model to the computer code as well as ensuring the model behaves as it was intended to behave also was a large part of the validation process. 3) The operational validation phase of the model involved determining the pertinent characteristics of the model, and identifying the importance of any differences between the real system and the model. Stress testing of the model was performed to determine how robust the model was regarding the value of the input parameters. Also, a

detailed sensitivity analysis was performed which involved a screening process that evaluated the elasticities of the parameters and a calculation of the main and interactive parameter effects through a 2⁴ experimental design. Validation, during the experimentation phase of the model, was achieved through inspection. Model output was compared qualitatively to information obtained from the real system in an attempt to achieve “closeness” between the real world and model output. Results and methodologies from this model were compared to other models to establish user confidence. Similar models have been used in Finland to achieve the same objectives (Marttunen 1992).

I used published parameter values for broad whitefish or a similar species such as lake whitefish whenever possible. In the absence of this information, input parameters and model output were compared to historical catch information and expert opinions. There was a general correspondence between the behaviour of the conceptual system and the real system. However, the data describing the behaviour of the real system were insufficient. Because of this, the model may or may not be an accurate replication of the mechanisms and dynamics that govern the broad whitefish population in the lower Mackenzie River. Therefore, using the model to predict actual effects of management actions is not recommended. However, if this model were to be used this way it should be used conservatively. Despite this, the model still provides an important heuristic tool for understanding the linkage between broad whitefish life history and exploitation. This should prove useful in the conceptualization of the effects of the fishery, the effects of other events that impact upon the most

sensitive model parameters, and as a basis for future development of more complex models.

Predicting the dynamics of natural populations has never been adequately resolved, even for renewable resources such as fisheries that have been the objects of scrutiny for decades. The problems which make parameter estimation a daunting challenge relate to the inability to identify and predict changes in the factors controlling dynamics, spatial and temporal variability of parameters, and even mechanisms of control (Sissenwine 1984). Models involved in fisheries management will always entail uncertainty because the model parameters are estimated with error and the actual fish populations usually exhibit random variations. Even if the model was exact and all parameters were known we still might encounter considerable uncertainty (Ruppert et al. 1985). In time, as more focused research is carried out on the broad whitefish of the lower Mackenzie River uncertainties involving parameter estimates and knowledge of the system will be minimized. However, due to the stochastic components within the system and the fish population uncertainty will always exist. Finally an inescapable conclusion from the existence of such uncertainty is that there will be surprises associated with virtually any management action (Holling 1978).

5.2 CONCLUSIONS

In the conceptual system the juvenile density-dependent parameters P7 and P8 were determined to be the most sensitive parameters. With parameter P7 being several orders of magnitude more sensitive than P8. These

parameters regulate the degree of density-dependent mortality that juveniles will encounter while in the freshwater lakes on the Tuktoyaktuk Peninsula which is thought to be the major rearing grounds for juvenile broad whitefish (Reist and Bond 1988, Chang-Kue and Jessop 1992). Many authors have proposed that juvenile mortality is the most important factor in population regulation. Viljanen (1988) stated that the central regulatory mechanisms of vendace populations lie in the little studied part of the life span between eggs and recruitment. The entire juvenile stage of the life cycle is important for population regulation in most species but the source of the variability in year-class strength is in the larval stage or very early juvenile stage (Elliott 1985 and 1990 b, Myers and Cadigan 1993). The ability of a fish population to pass through the larval period without excessive mortality is one of the primary factors determining the size of the resulting year class (Hjort 1914 as cited in Viljanen 1988).

Density dependence is assumed to operate in the juvenile stages of the life cycle. No empirical data are available to describe the effects density dependence may have on the juvenile portion of the life cycle therefore confidence regarding these parameter values is not high. Heuristic methods indicated that all forms of the function used to represent density-dependent mortality were highly sensitive. Therefore, in order to provide further understanding to the functioning of this system research would have to be directed towards the evaluation of the hypothesis that juvenile density dependence exists and plays a significant role in regulating the size of the broad whitefish population in the Mackenzie Delta. Attempting to answer this question

would be extremely expensive. It would involve a long-term venture requiring detailed documentation of many year classes of broad whitefish throughout their juvenile life cycle within the remote freshwater lake systems on the Tuktoyaktuk Peninsula. It is unlikely that ample monetary resources will be made available to study this phenomenon. Therefore, conclusions have been developed based on the more in depth analyses performed with the four next most sensitive parameters in the conceptual system.

The next most sensitive parameter in the conceptual system was the parameter that describes ratio of fishing mortality associated with upstream and downstream migrants (P12). This parameter was estimated through data collected during research studies conducted by the Department of Fisheries and Oceans in 1993-1994 (Tallman Unpublished Data). It was validated through face validity methodologies that involved the questioning of experts about the validity of the assumptions surrounding the mean parameter value.

The parameter of fecundity (P1) was nearly as sensitive as (P12) in the conceptual system. This parameter has been obtained empirically for the Mackenzie River broad whitefish therefore I am highly confident that this is an extremely important parameter governing the population dynamics of the broad whitefish in the Mackenzie Delta. This parameter should continue to be monitored into the future.

Interactive effects between the parameters P3 and P5 as well as between P1 and P3 have a significant effect on the conceptual system but to a much lesser degree than the previously mentioned effects of P12 and P1. The

parameter describing the level of egg survivability was estimated from valid literature sources for broad whitefish and other related species (Bogdanov 1991, Viljanen 1988, Helminen et al. 1993). The proportion of eggs hatching on the spawning grounds has not been studied in this system. It is assumed to be associated with climatic or environmental variables and therefore the proportion will likely be highly variable and remain a source of uncertainty from year to year. However, if the association between hatching success and environmental variables could be identified this source of uncertainty could be drastically reduced. The parameter describing the level of mortality associated with larvae that become trapped in the delta lakes (P5) is based on qualitative information (Lawrence et al. 1982). Insight into this parameter would also require a long-term strategy that would likely prove to be too expensive to carry out.

Parameters P2, P4, P6, P7, P9, P10, P11, P13 and P14 (Table 2) were less sensitive, therefore research into further understanding these parameters for broad whitefish would likely be less fruitful than research into parameters P12, P1, P3, and P5. Even though parameters P7 and P8 were the most sensitive in the conceptual system, research into the four previously mentioned parameters would be more economically feasible and likely provide more useful information to aid in the management of the Mackenzie River Broad Whitefish.

The systems analysis approach used herein is useful because it clearly indicated four areas where research should be focused. Research that is focused on the adult portion of the population and the fishery will do little to further our understanding and ability to manage this resource. Larval ecology,

juvenile ecology, and factors controlling fecundity are most important. This does not mean that the adult population and the fishery should be excluded from further study. Life-history parameters of the adult population and the level of exploitation should continue to be monitored. The model indicates fecundity to be an important parameter. However, because age at maturity and growth are directly related to fecundity and fecundity is directly tied to the output of the fishery all of the parameters mentioned above will have a direct impact on managing the fishery. Also, in spite of the fact that exploitation in the model was not nearly as sensitive as other parameters such as fecundity and density dependence, it is the one parameter that is known to control the standing stock size and as managers the total catch is under our control.

One of the most common intractable problems in fisheries management is to distinguish between the following two alternatives: 1) Are we harvesting a small fraction of a large stock ? or, 2) Are we harvesting a large fraction of a relatively small but productive stock ? (Ludwig and Walters 1981). Provided that the assumptions made in BDWT 1 regarding population regulation mechanisms and stock size are relatively accurate, the simulation results suggest that the fishing mortality experienced by the broad whitefish in this system is not significant at this time. This view agrees with conclusions made by Treble and Read (1994), Reist and Chang-Kue (1997), Treble and Tallman (1997). Thus, exploitation could be increased to some degree without any adverse effects to stock size. Even at conservative estimates of population size, the conceptual system is not negatively affected by fairly large increases in levels of exploitation.

Keeping in mind that the predictive ability of the model may be poor, it is likely that the geography of the area allows a sufficient number of spawners to escape fishing pressure and spawn successfully. The extensively channeled delta may provide many different routes for fish to migrate upstream. Some routes will be used by many subsistence and commercial fishermen but many other routes will be free of exploitation. Also, upstream near the areas of Fort McPherson and Tsiigehtchic where fish are most susceptible to exploitation due to a "bottle-necking" effect the extremely deep channels of the rivers (approximately 25 meters), likely allow a sufficient number of upstream migrants to avoid gillnets (which usually are set at a depth of approximately three meters). The geographic safe guards mentioned above may buffer the effects of over-exploitation by allowing a sufficient numbers of fish to escape and spawn each year. If this assumption is true, effort could be increased until catch levels reach a maximum.

Anderson (1995) states that (626, 063 kg), or approximately 275, 000 broad whitefish would have to be harvested in order for an export commercial fishery operation to break even at current market value prices ranging from \$0.66 to \$1.19. Given the large size of the system, its high productivity, and preliminary results given by BDWT 1, the lower Mackenzie River broad whitefish theoretically, should be able to withstand exploitation of this magnitude. However, commercial exploitation would have to become a priority and subsistence fishing would likely have to cease. Since, it is the mandate of both the FJMC and DFO, to preserve subsistence fisheries, commercial exploitation at

this level is not possible. Local commercial sales of surplus subsistence harvests are the best fishery development option (Anderson 1995).

5.3 FUTURE RESEARCH

1) Rearing grounds on the Tuktoyaktuk Peninsula and Richard's Island (P7 and P8)

A research study on the one or several of the freshwater systems on the Tuktoyaktuk Peninsula or Richard's Island should be conducted in order to gain insight into the most unknown and perhaps the most influential portion of the life cycle of broad whitefish in this system. The assumption of density dependence and its significance in these areas should be tested. The study should be long running (approximately ten years) in order to allow researchers to monitor growth and mortality of a single cohort from year 0+ through to maturity (i.e., approximately 8 +) in reference to other cohorts of different ages in the system. This should allow researchers to monitor the recruitment of fish into the adult population and shed light on some of the variables that affect this process. If the assumption of density dependence holds, this information will be of prime importance in understanding and predicting the population dynamics in this system. A research venture of this nature would most likely be associated with astronomical costs and therefore likely will never be executed. In light of this the greatest benefits would likely be gained by researching other parameters identified as important in the conceptual system.

2) Level of fishing mortality associated with upstream and downstream migrants (P12)

Development of a formalized methodology to measure and monitor the level of fishing mortality occurring during the upstream – pre-spawning migration compared to the level of fishing mortality occurring during the downstream - post-spawning migration would be very useful in managing this fishery. If it can be determined with a high level of confidence that fishermen are having a deleterious effect on the stock by intensely fishing the upstream – pre-spawning migration, managers could prevent further harmful effects to the fishery by implementing periods where fishing effort must be decreased or suspended. This would allow fish the chance to spawn a minimum of one time during their lifetime, thus having a significant contribution to the perpetuation of this population.

3) Larval mortality in delta lakes (P5)

Research into this parameter (larval mortality in delta lakes) will also require a long-term approach that will likely be extremely costly to carry out. Realistically, greater gains could be obtained by diverting resources to the study of parameters that are less costly to study.

4) Fecundity and the spawning grounds (P1 and P3)

Fecundity should be monitored on a consistent basis. Measurements for fecundity for each proposed stock (Point Separation, Peel, Arctic Red, and Fort Good Hope) should be taken. Stocks with the highest size-or age-specific fecundity are likely stocks which suffer the highest level of exploitation (Healey

1975), or may have had the greatest potential for harvest. The potential to withstand harvest will depend on the rate of change in fecundity within a stock with exploitation. Since the Fort Good Hope stock migrates the furthest and is presumably exploited the greatest number of times, females should exhibit higher size-or age-specific fecundities than the other stocks, especially the Point Separation stock.

Several research studies regarding spawning behaviour, spawning habitat, and the hatching success of the eggs should be conducted. Empirical measurements describing the proportion of eggs that will successfully hatch are needed for broad whitefish. This would require empirical measurements to be taken directly on the spawning grounds, which have not been precisely located to date. The location and observation of these sites alone would likely provide information on what types of variables are involved in regulating the hatching success of the eggs on the spawning grounds. Spawning behaviour such as whether or not broad whitefish exhibit territoriality, competition for mates, the degree of cannibalism of eggs on the spawning grounds, or the construction of nests or redds should also be studied. The answers to these questions will determine if broad whitefish experience density-dependent effects during the spawning process. If so, the amount of mortality on the spawning grounds may be able to be predicted thus aiding in the prediction of recruitment.

Studies should also focus on the amount of mortality that larvae may experience downstream. Mortality during this phase of the life cycle is likely to be highly variable and depend heavily on catastrophic events. However, the

degree of mortality should be looked at over several years to obtain a possible range of mortalities larvae may experience.

Other Research

Studies should also focus on obtaining a method to quantify and record the level of effort expended by the commercial and subsistence fishermen. The consistency of the technique and effort expended over time as a relative measure of CPUE should continue to be monitored in the future. Without this information catch values are less informative because of the concentration of these fish in space and time. The assumption of homogeneity in spawning fish in the upstream migration or the degree to which non-spawning (resting) fish mix with spawning fish should be explored. Also, further attempts should be taken to clearly identify individual spawning stocks. This would take into account the intensity of homing behaviour and the quantification of the degree of difference between stocks. This information is necessary before multiple stock management strategies can be developed such as the maximum-likelihood mixture model (Wood et al. 1987).

This study can be regarded as an important step in the research loop shown in Figure 4. After organizing and analyzing information obtained previous to this study, the model creates another more focused set of research priorities and hypotheses to test in the future. Such work will further aid the understanding and ability to manage this system.

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FORM5.FRM - 1

```
Sub Command2_Click ()
'Load form1
'form1.Show

Cls

End Sub

Sub startsim_Click ()
Call Main:

End Sub

Sub text1_change ()
Mata = Val(text1.Text)

End Sub

Sub Text2_Change ()
ss = Val(text2.Text)

End Sub

Sub Text3_Change ()
m1 = Val(text3.Text)

End Sub

Sub Text4_Change ()
' # of years the simulation will run
runtime = Val(text4.Text)

End Sub

Sub Text5_Change ()
psm = Val(text5.Text)

End Sub

Sub Text6_Change ()
F1 = Val(text6.Text)
End Sub

Sub Text7_Change ()
F2 = Val(text7.Text)
End Sub

Sub Text8_Change ()
F3 = Val(text8.Text)
End Sub
```

FORM7.FRM - 1

```
Sub Cancel_Click ()
    'Form2.Show
End Sub

Sub cCatch_Click ()
    form5!Text6.Text = form4!cCatch
End Sub

Sub Command1_Click ()
    form5.Show
    Unload form4

End Sub

Sub dCatch_Click ()
    form5!Text7.Text = form4!dCatch
End Sub

Sub eggssurv_Click ()
    form5!Text2.Text = form4!eggssurv
End Sub

Sub Form_Load ()
    Population.AddItem "500000"
    Population.AddItem "750000"
    Population.AddItem "1000000"
    Population.AddItem "2000000"
    Population.AddItem "5000000"
    Population.AddItem "10000000"
    Population.AddItem "20000000"
    eggssurv.AddItem "0.65"
    eggssurv.AddItem "0.7"
    eggssurv.AddItem "0.75"
    eggssurv.AddItem "0.8"
    eggssurv.AddItem "0.85"
    eggssurv.AddItem "0.9"
    eggssurv.AddItem "0.95"
    eggssurv.AddItem "0.99"

    owmort.AddItem "0.6"
    owmort.AddItem "0.7"
    owmort.AddItem "0.8"
    owmort.AddItem "0.9"
    owmort.AddItem "0.95"

    psmort.AddItem "0.01"
    psmort.AddItem "0.02"
    psmort.AddItem "0.03"
    psmort.AddItem "0.04"
    psmort.AddItem "0.05"
    psmort.AddItem "0.10"
    psmort.AddItem "0.15"
    psmort.AddItem "0.20"

    runtime.AddItem "5"
    runtime.AddItem "10"
    runtime.AddItem "20"
    runtime.AddItem "50"
    runtime.AddItem "75"
```

FORM7.FRM - 2

```
runtime.AddItem "100"
```

```
cCatch.AddItem ".05"  
cCatch.AddItem ".10"  
cCatch.AddItem ".15"  
cCatch.AddItem ".20"  
cCatch.AddItem ".25"  
cCatch.AddItem ".30"
```

```
dCatch.AddItem ".01"  
dCatch.AddItem ".05"  
dCatch.AddItem ".10"  
dCatch.AddItem ".15"  
dCatch.AddItem ".20"  
dCatch.AddItem ".25"  
dCatch.AddItem ".30"  
dCatch.AddItem ".35"  
dCatch.AddItem ".40"  
dCatch.AddItem ".50"
```

```
iCatch.AddItem ".05"  
iCatch.AddItem ".10"  
iCatch.AddItem ".15"  
iCatch.AddItem ".20"  
iCatch.AddItem ".25"  
iCatch.AddItem ".30"  
iCatch.AddItem ".35"  
iCatch.AddItem ".40"  
iCatch.AddItem ".45"  
iCatch.AddItem ".50"  
End Sub
```

```
Sub iCatch_Click ()  
form5!Text8.Text = form4!iCatch  
End Sub
```

```
Sub owmort_Click ()  
form5!Text3.Text = form4!owmort  
End Sub
```

```
Sub Population_Click ()  
form5!Text1.Text = form4!Population  
End Sub
```

```
Sub psmort_Click ()  
form5!Text5.Text = form4!psmort  
End Sub
```

```
Sub runtime_Click ()  
form5!Text4.Text = form4!runtime  
End Sub
```

MAIN_S.BAS - 1

```
Global juvmat() As Double
Global ss As Single
Global psm As Single
Global m1 As Single
Global matrix() As Single
Global t As Integer
Global F1 As Single
Global F2 As Single
Global F3 As Single
Global Ct As Single
Global seedA!
Global seedB!
Global seedC!
Global seedD!
Global seedE!
Global seedF!
Global seedG!
Global seedH!
Global seedI!
Global seedJ!
Global seedK!
```

Sub Main ()

Main:

```
matage = 8
reps = 600
ReDim matrix(runtime, 4)
ReDim juvmat(matage)
ReDim bigmat(runtime) As Single
```

```
For j = 1 To runtime
    bigmat(j) = 0
Next j
```

InitMata = Mata

```
For simreps = 1 To reps
    Mata = InitMata
    For t = 1 To runtime
```

```
        matrix(t, 1) = t
        matrix(t, 2) = Mata
```

'LIST OF SEED VALUES

```
seedA! = (-5005 + t + simreps)
seedB! = (-6008 + t + simreps)
seedC! = (-7012 + t + simreps)
seedD! = (-8010 + t + simreps)
seedE! = (-9013 + t + simreps)
```


MAIN_S.BAS - 2

```
seedF! = (-10015 + t + simreps)
seedG! = (-11016 + t + simreps)
seedH! = (-12014 + t + simreps)
seedI! = (-13007 + t + simreps)
seedJ! = (-14002 + t + simreps)
seedK! = (-15024 + t + simreps)
```

'MAIN PROGRAM

```
Call egg_survival:
Call larval_migration:
Call juv_mort_T:
Call Tuklake_larvae:
Call juvenileM:
Call exploitation_MatV:
Call Mix_W_Mat_Pop:
Call prespawn_exploitation:
Call Postspawn_Mortality:
Call postspawn_exploitation:
Call Overwintering_Pop:
```

Ct = (C1 + C2 + C3 + C4)

'Call Graphics:

```
Mata = matat2.
If Mata < 0 Then Stop
```

```
matrix(t, 3) = matve
matrix(t, 4) = Ct
```

Call savefile:

Next t

```
For j = 1 To runtime
  bigmat(j) = matrix(j, 2) + bigmat(j)
Next j
```

Next simreps

```
For j = 1 To runtime
  bigmat(j) = bigmat(j) / reps
Next j
```

```
Open "run22.prn" For Output Access Write Lock Write As 3
For j = 1 To runtime
  Write #3, bigmat(j)
Next j
```

MAIN_S.BAS - 3

Close #3

'GraphA.Show

Beep

Beep

Beep

End Sub

MOD1_S.BAS - 1

Global hatch As Single

Global eggs As Single

'hatch will determine the amount of eggs surviving to hatch
Sub egg_survival ()

egg_survival:

 If t = 1 Then

 matase2 = mata / 4

 Else matase2 = matase2

 End If

 'density dependance on spawning grounds (Beverton Holt).

 randnum! = (GASDEV(seedA!))

 fecund = ((randnum! * 14803) + 14500)

 a = fecund

 b = 220000000000#

 eggs = (((matase2) / 2)) * fecund / (1 + ((a / b) * (matase2) / 2))

 'first div. by 2 is for sex ratio the second div. by 2

 'is for the alternate year spawning.

 randnum! = (GASDEV(seedB!)) 'varied 10% of the mean.

 ssr = (randnum! * (.1 * ss)) + ss

 hatch = eggs * ssr

 hatch = hatch

End Sub

MOD2_S.BAS - 1

Global larvae As Double
Global LarvaeT As Double
Global larvaeS As Double

'determines % larvae successful and % trapped
,

Sub larval_migration ()
larval_migration:

 larvae = hatch

 '% becoming trapped in delta lakes

 randnum! = (GASDEV(seedC!)) 'sd is 10% of the mean.

 LarvaeT = larvae * ((randnum! * (.1 * .2)) + .2)

 LarvaeT = .2 * larvae

 '.2= 20% reaching delta lakes

 '% reaching lakes for rearing

 larvaeS = larvae - LarvaeT

End Sub

MOD3_S.BAS - 1

Global juv_dl As Double

'o.w. mortality of yoy in delta lakes (trapped)

Sub juv_mort_T ()

juv_mort_T:

 'juveniles from lakes after 1 winter

 randnum! = (GASDEV(seedD!)) 'sd is 10% of the mean.

 mlr = (randnum! * (.1 * m1)) + m1

 juv_dl = larvaeT * (1 - mlr)'high mort. due to predation

End Sub

MOD4_S.BAS-1

```
For i = matage To 1 Step -1
  juvmat(i) = juvmat(i - 1) * ((JuvKM(i, 1) * (Exp(JuvKM(i, 2)
* juvmat(i - 1)) + (1 - JuvKM(i, 1)))) - M)
  If juvmat(i) < 0 Then juvmat(i) = 0
Next i
```

```
juvmat(0) = juv_1
```

```
If t <> 1 Then
juvmat(1) = juvmat(1) + juv_dl
End If
```

```
' maturity occurs at 8 years of age, this must be made
'stochastic later on!!!!
' MatV mature ind. leaving lakes to spawn
```

```
MatV = juvmat(matage)
End Sub
```

Global juv_succ As Double

```
'mortality rate of yoy during first year in lakes
```

```
Sub Tuklake_larvae ()
Tuklake_larvae:
```

```
  juv_succ = larvaeS
  '60 days travelling 1 - 19% (avg of 10% mort.)overall
mortality(Bogdanov)
  'level of success depends on chance of encountering
  'ice or log jam or other catastrophic events.
```

```
  dailyM = .1 'with a sd chosen as 10% of the mean
```

```
  randnum! = (GASDEV(seedE!))
  dailyMr = (randnum! * (.1 * dailyM)) + dailyM
```

```
For d = 1 To 60
  juv_succ = juv_succ * (1 - dailyMr)
Next d
```

```
  juv_1 = juv_succ
```

```
End Sub
```

MOD5_S.BAS - 1

Global MatV
Global matage

Dim JuvKM() As Single
Dim juv_1b, juv_2b, juv_3b, juv_4b, juv_5b, juv_6b, juv_7b
Dim juv_2, juv_3, juv_4, juv_5, juv_6, juv_7, juv_8
Dim ddl, dd2, dd3, dd4, dd5, dd6, dd7, dd8

'calculate juvenile mort. in lakes from years 1 to maturity
(inverted B-H eq.)

'Age structure in the juvenile population!

Sub juvenileM ()
juvenileM:

ReDim JuvKM(matage, 2)

JY1A = .7
JY1B = 8
JY2A = .65
JY2B = 6.5
JY3A = .55
JY3B = 4
JY4A = .5
JY4B = 3
JY5A = .4
JY5B = 2

randnum! = (GASDEV(seedF!)) 'parameters sd is chosen at
10% of the mean

JY1Ar = (randnum! * (.1 * JY1A)) + JY1A
JY1Br = (randnum! * (.1 * JY1B)) + JY1B
JY2Ar = (randnum! * (.1 * JY2A)) + JY2A
JY2Br = (randnum! * (.1 * JY2B)) + JY2B
JY3Ar = (randnum! * (.1 * JY3A)) + JY3A
JY3Br = (randnum! * (.1 * JY3B)) + JY3B
JY4Ar = (randnum! * (.1 * JY4A)) + JY4A
JY4Br = (randnum! * (.1 * JY4B)) + JY4B
JY5Ar = (randnum! * (.1 * JY5A)) + JY5A
JY5Br = (randnum! * (.1 * JY5B)) + JY5B

JuvKM(1, 1) = JY1Ar 'JY1A
JuvKM(1, 2) = JY1Br * -.000000001 'JY1B
JuvKM(2, 1) = JY2Ar 'JY2A
JuvKM(2, 2) = JY2Br * -.000000001 'JY2B
JuvKM(3, 1) = JY3Ar 'JY3A
JuvKM(3, 2) = JY3Br * -.000000001 'JY3B
JuvKM(4, 1) = JY4Ar 'JY4A
JuvKM(4, 2) = JY4Br * -.000000001 'JY4B

For i = 5 To matage
JuvKM(i, 1) = JY5Ar 'JY5A
JuvKM(i, 2) = JY5Br * -.000000001 'JY5B
Next i

```

If t = 1 Then
  For i = 0 To matage
    juvmat(i) = 0
  Next i
End If
  M = .15 'this is density independent mortality

```

MOD6_S.BAS-1

```

Global MatVE As Single
Global C1 As Single

'calculates the amount of mortality from fishing the
'virgins leaving the lakes
'
Sub exploitation_MatV ()
exploitation_MatV:
  'C1 'combined coastal catches, mature virgins escaping.

  randnum! = (GASDEV(seedG!))
  Flr = (randnum! * (.2 * F1)) + F1

  C1 = MatV * Flr 'C1 is varied 25%

  MatVE = MatV - C1
End Sub

```

MOD7_S.BAS-1

```

Global MatA As Single
Global MatAS As Single
Global MatASE1 As Single
Global C2 As Single

'virgins escaping fishing mix with existing mature component
'of population
'All spawners are now subjected to fishing pressure throughout
'the delta, inparticular Horseshoe Bend
'
Sub Mix_W_Mat_Pop ()
Mix_W_Mat_Pop:
  ' C2 'combined commercial and domestic catch in entire delta

  'MatA 'mature individuals from input of initial pop. size
  'MatAS ' # of spawners for that year.
  'MatASE1 ' # of spawners escaping the fishery1

  MatAS = ((MatA * .5) + MatVE)

  randnum! = (GASDEV(seedH!))
  F2r = (randnum! * (.2 * F2)) + F2

```



```
C2 = MatAS * F2r 'F2 is given a 20% sd.  
MatASE1 = MatAS - C2
```

```
End Sub
```

MOD8_S.BAS-1

```
Global MatASE2 As Single  
Global C3 As Single  
Global F3r As Single
```

```
'fish escaping the fisheries in the delta will be subjected to  
'fisheries before reaching their spawning grounds  
,
```

```
Sub prespawn_exploitation ()  
prespawn_exploitation:  
  'MatASE2 ind. escaping fisheries south of HB
```

```
  randnum! = (GASDEV(seedI!))  
  F3r = (randnum! * (.2 * F3)) + F3
```

```
  C3 = MatASE1 * (F3r * .9) 'C3 is catch during upstream  
migration  
  MatASE2 = MatASE1 - C3
```

```
End Sub
```

MOD10_S.BAS-1

```
Global MatPSE As Single  
Dim MatPS As Single  
Global C4 As Single
```

```
'after spawning ind. will be subjected to fishing Mortality  
'at the same places as on the upstream migration however at  
'a lower intensity  
,
```

```
Sub postspawn_exploitation ()  
postspawn_exploitation:  
  C4 = ((F3 * .3) * MatPS) 'downstream exploitation  
  MatPSE = MatPS - C4
```

```
'Ct is the total annual catch to be graphed
```

```
End Sub
```

```
'after spawning fish will suffer a certain amount of mortality  
'this will be constant for all ind. for now because there is no  
stock structure  
'in the model yet  
,
```

```
Sub Postspawn_Mortality ()
```

Postspawn_Mortality:

```
randnum! = (GASDEV(seedJ!))  
psmr = (randnum! * (.1 * psm)) + psm '40% variation....
```

```
MatPS = (MatASE2) * (1 - psmr)'amount of post spawning  
mortality
```

End Sub

MOD11_S.BAS - 1

```
Global runtime As Integer  
Global MatAT2 As Single
```

```
'the post spawners that escaped fishing and post spawning  
mortality
```

```
'now return to the overwintering population in the delta
```

```
Sub Overwintering_Pop ()
```

```
randnum! = (gasdev(seedK!))  
OWM = .35 ' .35 assumes 15% OW mortality to resting  
fish
```

```
OWMR = (randnum! * (.1 * OWM)) + OWM
```

```
MatAT2 = MatPSE + (MatA * OWMR) ' pop. size at start of next  
year
```

End Sub

MOD12_S.BAS. - 1

```
Static Function GASDEV! (IDUM!)
```

```
Static iset, gset
```

```
If iset = 0 Then
```

```
Do
```

```
V1 = 2! * Ran1(IDUM!) - 1!
```

```
V2 = 2! * Ran1(IDUM!) - 1!
```

```
R = V1 ^ 2 + V2 ^ 2
```

```
Loop While R >= 1! Or R = 0!
```

```
FAC = Sqr(-2! * Log(R) / R)
```

```
gset = V1 * FAC
```

```
GASDEV = V2 * FAC
```

```
iset = 1
```

```
Else
```

```
GASDEV = gset
```

```
iset = 0
```

```
End If
```

End Function

Static Function Ran1! (IDUM!)

```
Dim R(97)
z1& = 259200
IA1& = 7141
IC1& = 54773
RM1 = .0000038580247
M2& = 134456
IA2& = 8121
IC2& = 28411
RM2 = .0000074373773
M3& = 243000
IA3& = 4561
IC3& = 51349
```

```
If IDUM! < 0 Or IFF = 0 Then          'As above, initialize on
first call even if idum! is not negative
  IFF = 1
  IX1& = (IC1& - IDUM!) Mod z1&      'Seed the first routine
  IX1& = (IA1& * IX1& + IC1&) Mod z1&
  IX2& = IX1& Mod M2&              'and use it to seed the 2nd
  IX1& = (IA1& * IX1& + IC1&) Mod z1&
  IX3& = IX1& Mod M3&              'and 3rd order routines      'fill table
with sequential uniform deviates
  For J = 1 To 97                    'generated
by the first two routines
  IX1& = (IA1& * IX1& + IC1&) Mod z1&
  IX2& = (IA2& * IX2& + IC2&) Mod M2&
  R(J) = (CSng(IX1&) + CSng(IX2&) * RM2) * RM1 'low and
high order pieces combined here
  Next J
  IDUM! = 1
End If
  IX1& = (IA1& * IX1& + IC1&) Mod z1&      'except when
initializing, this is where we start
  IX2& = (IA2& * IX2& + IC2&) Mod M2&      'generate the next
number for each sequence
  IX3& = (IA3& * IX3& + IC3&) Mod M3&
  J = 1 + Int((97 * IX3&) / M3&)           'use third
sequence to get an integer b/w 1 and 97
  If J > 97 Or J < 1 Then Introform.Print "abnormal exit": Exit
Function
  Ran1 = R(J)                          'return that
table entry
  R(J) = (CSng(IX1&) + CSng(IX2&) * RM2) * RM1 'and refill it

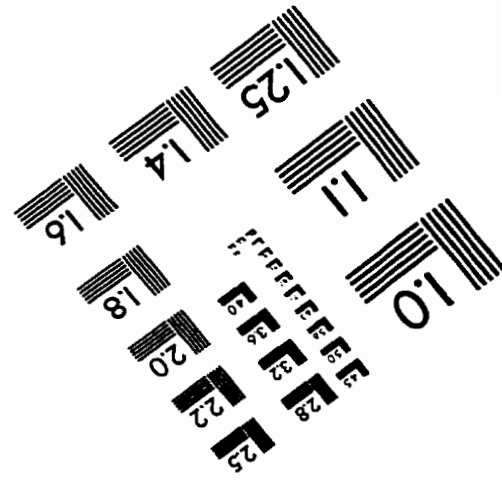
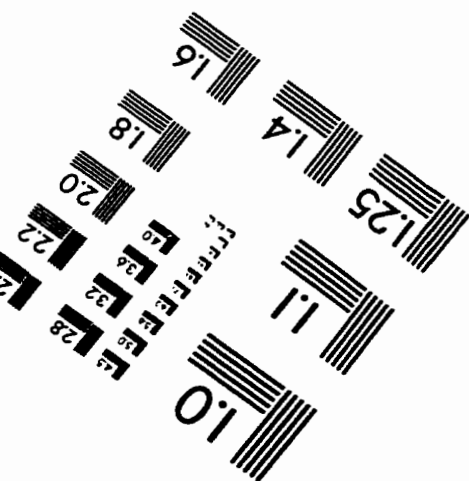
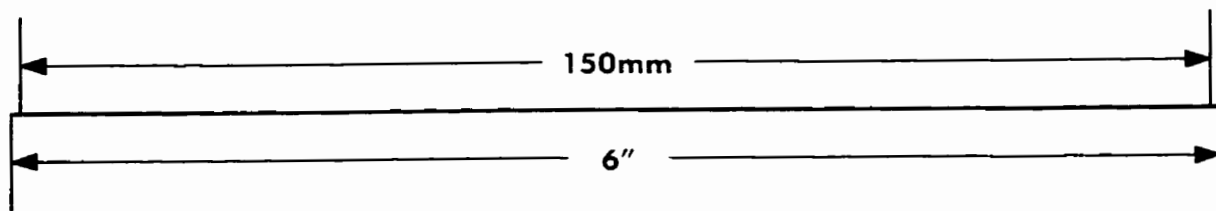
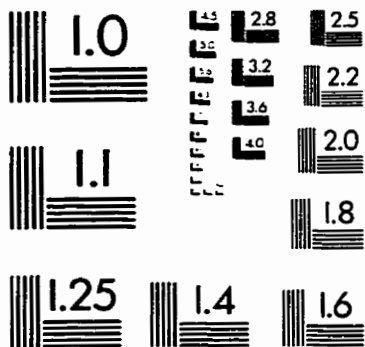
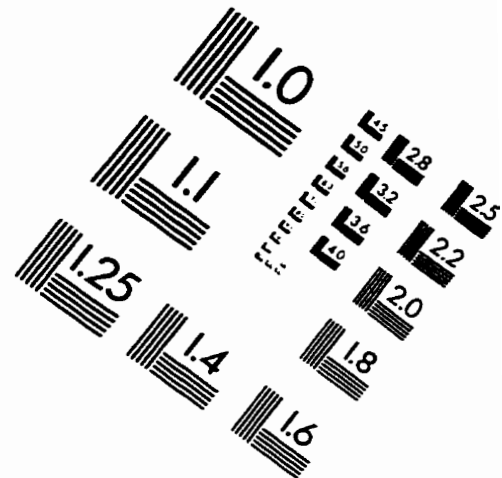
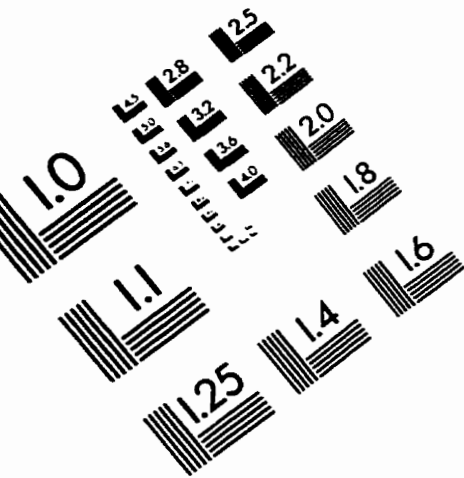
End Function
```

MOD13_S.BAS - 1

```
Dim filenum As Integer  
Dim recordlen As Long
```

```
Sub savefile ()  
    filenum = FreeFile  
    Open "fish3.fil" For Output Access Write Lock Write As filenum  
    Write #filenum, "runtime", "mata", "1st time S", "catch"  
    For i = 1 To runtime  
        Write #filenum, matrix(i, 1), matrix(i, 2), matrix(i, 3),  
matrix(i, 4)  
    Next i  
    Close filenum  
End Sub
```

IMAGE EVALUATION TEST TARGET (QA-3)



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