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EVALUATION OF BIOENERGETICS MODELING IN THE STUDY OF PREDATOR-PREY DYNAMICS IN MINNESOTA WATERS OF LAKE SUPERIOR[1]

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Abstract.--Lake Superior's fish community has undergone dramatic changes since the mid-1950's, with major shifts in the forage base, invasion of exotics, and the decline of lake trout. Predator species have been introduced, and many of the predator stocks are maintained by stocking. The impact of these stocked fish on the forage base, and the ability of the forage base to sustain projected stocking levels are unknown. The most current information on fish populations in Lake Superior has been collected by biologists in three states, several tribes, the province of Ontario, and the U. S. Fish and Wildlife Service. Much of the information, however, is unpublished or in publications with limited distribution. Bioenergetics modeling can use basic population data for answering research and management questions about predator-prey dynamics, stocking quotas, and forage requirements. The objectives of this study were: 1) to compile data on the major salmonines in Minnesota waters of Lake Superior, as input for a bioenergetics model; 2) to estimate salmonine predation on prey populations in Minnesota waters through modeling simulations; 3) to conduct sensitivity analyses of the bioenergetics model; and 4) to prioritize data requirements for input to the bioenergetics model. Estimates of consumption by predator stocks in 1989 totaled 2,814 metric tonnes of rainbow smelt and 249 metric tonnes of coregonines, which greatly exceeded biomass plus production estimates of forage species (about 100 metric tonnes of rainbow smelt and 85 metric tonnes of coregonines). Discrepancies could be due to underestimates of forage fish biomass or inaccuracies in data on predators. Predator consumption estimates in the bioenergetics simulations were most influenced by values used for predator population abundance, weights, diets, and prey caloric densities. Further data acquisition should focus on the forage base biomass and production, predator age and growth, periodic diet monitoring, predator population abundances, and mortality rates.

Introduction

Lake Superior's fish populations are supplemented by extensive salmonine stocking, but quantitative information about existing stocks and community interactions is incomplete and difficult to obtain. Traditional management strategies, aimed at one species or game species only, were inadequate in this dynamic ecosystem. Efforts focused on rehabilitating fish stocks when populations showed signs of distress, emphasizing the trial-and-error nature of fisheries science at that time. The increased stocking desired by anglers sometimes conflicted with managing toward a renewable and stable fish community (Spangler et al. 1987). Christie et al. (1987) and Spangler et al. (1987) recommended a community analysis to predict the effects of management actions on the species assemblages. Management strategies are now focusing on this community approach, so that healthy fish communities can be maintained without the high level of risk previously encountered.

Bioenergetics modeling is a powerful tool for answering questions about predator-prey dynamics, stocking quotas, and the forage requirements of predators (Christie et al. 1987; Hewett and Johnson 1987). Bioenergetics modeling uses fish physiology, temperature, growth (weight at age), diet composition, prey caloric content, and population abundance data to estimate food consumption (Kitchell 1983; Hewett and Johnson 1987). Sensitivity analysis (Kitchell 1983) can be used to evaluate existing data, and identify and prioritize future data needs. Variation in number and strain of stocked salmonines, and the unknown extent of natural reproduction has made standing stock estimation difficult in Lake Superior. However, estimating the forage requirements of Minnesota-stocked fish is a manageable goal. Results can be used to adjust stocking quotas and harvest regulations to ensure a stable fishery.

A review of the recent history of the fish community in Lake Superior emphasizes many changes and interactions. The fish community has undergone dramatic changes since the mid-1950's beginning with the invasion of the sea lamprey *Petromyzon marinus*, and the decline of lake trout *Salvelinus namaycush* and lake herring *Coregonus artedii*. Rainbow smelt *Osmerus mordax*, which invaded in the mid-1950's and boomed in the 1960's, replaced declining lake herring as the principal lake trout forage (MacCallum and Selgeby 1987; Busiahn 1990; Hansen 1990). Subsequent lake rehabilitation programs included harvest restrictions on lake herring and lake trout, sea lamprey control, and lake trout stocking (Lawrie and MacCallum 1980; Walters et al. 1980; Busiahn 1990). Rainbow smelt stocks have fluctuated and are now in a severe decline lake-wide, while lake herring are making a strong comeback (Schreiner and Morse 1990). The primary method of harvest has shifted from the traditional commercial fishery which targeted native lake trout and lake herring, to an economically important recreational fishery targeting lake trout and introduced salmonines.

Lake Superior has lower productivity than the other Great Lakes, so the sustainable yields of predator and prey fish are lower, and the likelihood of over-harvesting or over-stocking is greater. In spite of this risk, stocking quotas have been determined by historical production levels and hatchery capacities rather than by an understanding of community dynamics. Lake trout, chinook salmon *Oncorhynchus tshawytscha*, steelhead and Kamloops strain rainbow trout *O. mykiss*, and Atlantic salmon *Salmo salar* have been stocked in Minnesota waters in recent years. While predator stocks have increased, the structure of the forage base has changed greatly, and predator-prey interactions are poorly understood (Busiahn 1990).

Lake trout growth has decreased in many areas of the lake during the past 15 years, probably because of changes in the forage base (Hansen 1990). The small size and inshore distribution of rainbow smelt may make them of lower value than lake herring as forage for lake trout (Jacobson et al. 1987). Lake herring were historically a preferred lake trout forage, with pelagic lake-wide distribution. Since the resurgence of lake herring populations, however, lake trout have shown a reluctance to return to lake herring as a forage base (Hansen 1990).

Fish population information from Lake Superior has been collected by biologists in three states, several tribes, the province of Ontario, and the U. S. Fish and Wildlife Service. Because of agency differences, data sets are sometimes inconsistent and difficult to compare. Lakewide impacts from different management strategies are difficult to evaluate because the effects are cumulative and stocks are poorly defined. Rapid assessment methods and prioritizing data acquisition are paramount, given the size and complexity of Lake Superior.

Objectives of this study were: 1) to compile available data on lake trout, coho salmon *Oncorhynchus kisutch*, chinook salmon, steelhead and Kamloops strains of rainbow trout, Atlantic salmon, and forage species in the Minnesota waters of Lake Superior for input into a bioenergetics model; 2) to estimate salmonine predation on prey populations through modeling simulations; 3) to conduct sensitivity analyses of the bioenergetics model; and 4) to identify and prioritize data needs for increased accuracy in bioenergetics model simulations.

Study Area

The Minnesota waters of Lake Superior encompass 572,900 hectares, which have been divided into three management zones (Figure 1). The Minnesota shoreline is rocky and steep, and extends 304 km between Duluth and the Canadian border. Eighty-seven percent of the surface area represents water with depth greater than 73 m, and thermal stratification occurs in late July, when maximum surface temperatures

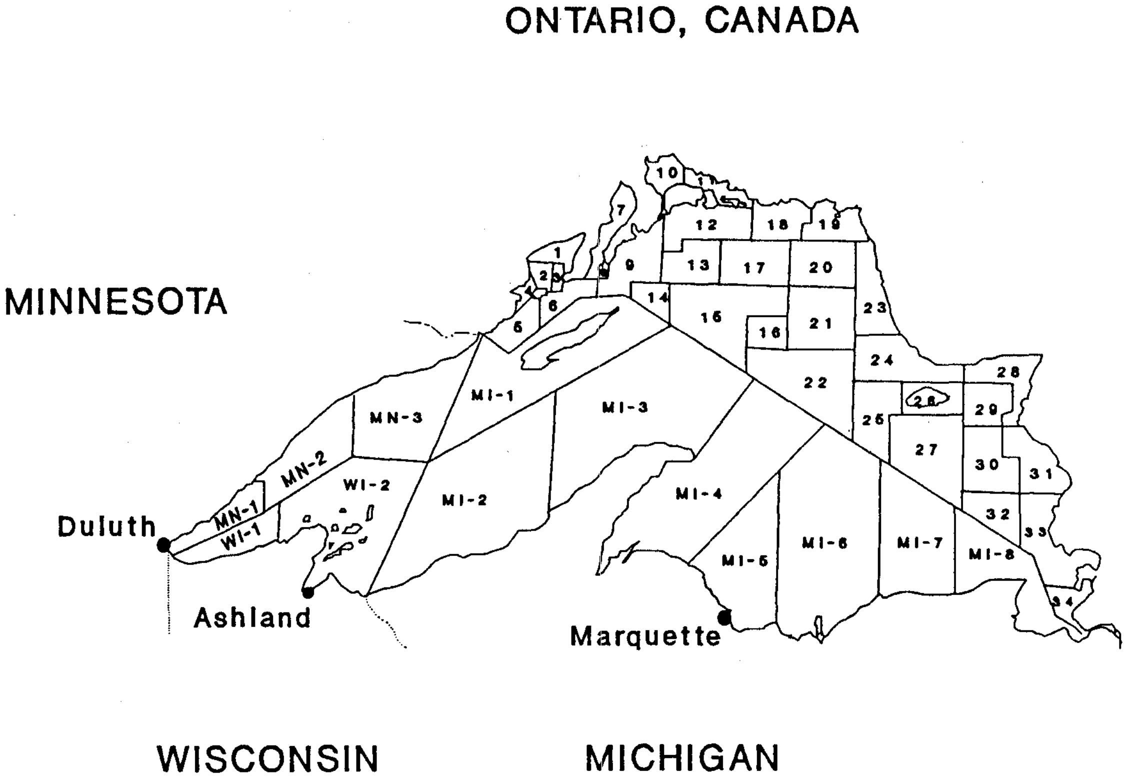

Figure 1.--Lake Superior management zones. Management zones in Minnesota waters include MN-1, MN-2, and MN-3 (Lake Superior Lake Trout Technical Committee 1986).

range from 12.6°C to 16.8°C (Close et al. 1984).

Most of Minnesota's North Shore streams are inaccessible for spawning by anadromous species due to barrier falls and gravel bars at the stream mouths. Stream productivities are low, resulting from unproductive soils, rocky terrain, erratic flows, and winter ice scouring (Close et al. 1984). Lake Superior productivity is also low for similar reasons, in addition to low temperatures.

Minnesota waters of Lake Superior support a commercial fishery for rainbow smelt, lake herring, and chub (bloaters *Coregonus hoyi* and some kiyi *C. kiyi*). The sport fishery includes (in decreasing order of harvest) lake trout, coho salmon, chinook salmon, rainbow trout, and Atlantic salmon. Brown trout *Salmo trutta* and Siscowet trout *Salvelinus namaycush siscowet* are taken occasionally, and pink salmon *Oncorhynchus gorbuscha* and brook trout *Salvelinus fontinalis* are rarely caught (Morse 1989). Lake trout, chinook salmon, Kamloops strain rainbow trout, and Atlantic salmon populations are maintained primarily by stocking, although native (naturally reproducing) lake trout are becoming more abundant. Naturalized coho salmon migrate from spawning streams in Wisconsin and Michigan to feed in Minnesota waters.

Literature Review and Data Compilation

A literature search was conducted to gather life history information and data required for bioenergetics modeling of the primary fish species in Minnesota waters of Lake Superior. Target species were lake trout, chinook salmon, coho salmon, steelhead and Kamloops strain rainbow trout, Atlantic salmon, sea lamprey, and forage species. The bibliography in Hewett and Johnson (1987), and the literature file maintained in the Minnesota Department of Natural Resources (MNDNR) Fisheries Research office in Duluth were preliminary information sources.

Additional information was gathered through meetings with biologists from various resource agencies, including MNDNR, University of Minnesota, University of Wisconsin Sea Grant Program, Great Lakes Indian Fish and Wildlife Commission, Michigan Department of Natural Resources, State University of New York, and the U. S. Fish and Wildlife Service: National Fisheries Research Center - Great Lakes in Ashland, Wisconsin. Much of the current data on these species has not yet been published in peer-reviewed journals, so acquisition of file data, and references to in-house publications were essential. Much of this information is tabulated in Appendices of this report.

The most current data from fish occupying Minnesota waters of Lake Superior were compiled whenever possible. Data from fish in other parts of Lake Superior were used when Minnesota data were unavailable, and data from other waters were compiled when Lake Superior data were unavailable. Throughout this study, naturally reproduced lake trout and coho salmon were called native lake trout and naturalized coho salmon. Steelhead are the naturalized anadromous rainbow trout which were introduced into Lake Superior in 1895 (MacCrimmon 1971), and some steelhead are stripped at the French River Hatchery and stocked as fry into North Shore streams. Kamloops strain rainbow trout are an anadromous hatchery strain currently being stocked as yearlings. Because steelhead and Kamloops strains are stocked at different sizes, are managed separately, and were modeled separately, they are distinguished as separate groups in this study. The two strains will hereafter be referred to as simply "steelhead" and "Kamloops."

Lake trout

Temperature.--Lake trout occupy a range of temperatures, depending on genetic strain (Elrod and Schneider 1987), life stage, season, and geographic location (Coutant 1977; Martin and Olver 1980; Wismer and Christie 1987; Table A2). Temperatures occupied in nature are often colder than the preferred temperatures determined in a laboratory (McCauley and Tait 1970; Elrod and Schneider 1987). Adult temperature preferences in Lake Superior are unknown, but Kitchell and Breck (1980) used 12°C as the maximum summer temperature, and Stewart (1980) used 10°C as the maximum summer temperature for lake trout in bioenergetics modeling of Lake Michigan.

Temperatures available to salmonines in this study were estimated from temperatures of Lake Superior water entering the French River Hatchery through an intake pipe located at a depth of 18.3 m (Table A1). Some variation in available summer temperatures was assumed, and the maximum summer temperature used in lake trout modeling was 10°C (Table A7). Winter temperatures dropped to 1.1°C. Stocked lake trout were assumed to occupy the same temperatures as native lake trout.

Age and Growth.--Lake trout are stocked into Lake Superior as fall fingerlings (about 8 g) or spring yearlings (about 30 g), and adults greater than age 15 are rarely seen. Weights at each age are needed for bioenergetics modeling, but often only lengths were reported in the literature. Length-weight relationships were calculated from available data, or obtained from other sources, for use when weights were not reported (Table B2; Figure B1).

Growth rates of lake trout varied considerably between Lake Huron (Fry 1953), Lake Michigan (VanOosten and Eschmeyer 1956; Stewart 1980), and Lake Superior (Dryer and King 1968; Martin and Olver 1980; Schreiner et al. 1989). Growth rates also varied historically in Lake Superior (Rahrer 1967; Dryer and King 1968; Hansen 1990). Variation was correlated with changes in the forage base, changes in lake trout strain as native stocks were eliminated and hatchery strains were introduced, and gear bias (Dryer and King 1968; Schreiner et al. 1989; Table B1).

Size at age was obtained for Minnesota stocked lake trout which had fin clips indicating year-class (Table B1). Data were collected by commercial fishermen and MNDNR personnel using large mesh gill nets (11.4 - 14.0 cm stretch mesh) in May and September, and by MNDNR personnel using small mesh gill nets (3.8 - 6.4 cm stretch mesh) in July and August. Individual weights were available for fish captured in small mesh nets, and weights were estimated for large fish using length-weight relationships (Table B2). The 1989 length-weight relationship of stocked lake trout in Minnesota was essentially the same as the length-weight relationship developed for lake trout in all of Lake Superior (Figure B1). Weights used in simulations (Table B7) approximated the weight at age of Minnesota fish (Table B1).

Native and stocked lake trout were modeled separately because the younger fish appear to grow at different rates. Size at age determinations for Minnesota's native lake trout were unavailable, but young native lake trout tended to be smaller than stocked fish in zone MI-3 (National Fisheries Research Center, Ashland, unpublished; Table B1). An extensive but unanalyzed set of native lake trout scales is housed at the Lake Superior Area office of the MNDNR. The maximum weight attained in simulations of stocked and native lake trout was 4,200 g.

Diet.--Lake trout diet varies with season, life stage, and geographic location (Martin and Olver 1980), but the primary diet item in Minnesota waters of Lake Superior is rainbow smelt (Table C1). Historical changes in diet are well documented in the Great Lakes as the forage base has changed (Lawrie 1978; Hansen 1990). Diet of lake trout was compiled into five categories for modeling purposes: rainbow smelt; coregonines (primarily lake herring, with some chubs); insects; crustaceans (primarily opossum shrimp *Mysis relicta*); and other small salmonines (Table C1). The most recent diet information from gill net assessments in 1990 suggests that consumption of lake herring by lake trout may be increasing (D. Schreiner and S. Morse, MNDNR, personal communication).

Caloric densities (calories/g wet weight) of diet items were not widely reported. The caloric value for bloaters in Rottiers and Tucker (1982) was used for coregonines (Table C3) because no value for lake herring could be found. Caloric density for opossum shrimp could not be found, so a value for Amphipoda (also subclass Malacostraca, but a different order) was used (Cummins and Wuycheck 1971). The caloric density used for small salmonines was an intermediate value from those reported by Stewart et al. (1983). The fraction of indigestible material in the prey items was taken from the sample data file supplied with the bioenergetics model: fish and crustaceans = 0.033; and insects = 0.100 (Hewett and Johnson 1987).

Mortality.--Stocking records of fall fingerlings and spring yearlings provided initial population estimates for stocked lake trout (Table D1). A mean of 335,547 lake trout (fingerlings and yearlings) were stocked annually from 1975 to 1989. The relative catch rate of stocked versus native lake trout of all ages captured in gill nets allowed an estimate of native lake trout abundance (D. Schreiner, MNDNR, personal communication; Table D2). The age 0 native lake trout population size was calculated assuming an 89.8% mortality rate for age 0 lake trout (Ebener et al. 1990).

All lake trout mortality estimates in table D3 are a combination of fishing mortality and natural mortality (including mortality from sea lamprey). Mortality rates for age 0 to age 6 lake trout in Minnesota waters were assumed to be the same as those reported for Wisconsin management zone WI-2 (Ebener et al. 1990; Table D3). Mortality rates for lake trout ≥ age 7 were means from recent estimates calculated by Schreiner et al. (1988, 1989, 1990) using data from large mesh gill nets (Table D3).

Spawning.--Lake trout in Minnesota waters of Lake Superior reach maturity at ages 6 to 7 (males), or age 8 (females) (Schreiner et al. 1990). For modeling purposes, first spawning was assumed to occur in late October at age 7.

The bioenergetics model assumes that weight loss due to spawning is a fixed proportion of the body weight, and this weight is subtracted on a particular day of the year for all cohorts older than the first spawning cohort. The model assumes that this proportional weight loss is the same for all mature cohorts, and that all individuals spawn (Hewett and Johnson 1987). I used 6.8% as the average spawning weight loss, which is a value calculated from Lake Michigan lake trout (Stewart et al. 1983).

Chinook salmon

Temperature.--Literature sources for the temperature preference of chinook salmon in Lake Superior were not found. Chinook salmon preferred temperatures of 6°C to 17.3°C in other waters (Table A3), but in Lake Superior they appear to occupy temperatures similar to lake trout, with an annual mean approximating 5.5°C (C. Bronte, National Fisheries Research Center, personal communication). Temperatures used in simulations were similar to those for lake trout, ranging from 1.1°C to 10.0°C (Table A7).

Age and Growth.--Chinook salmon fry and fingerlings are stocked into North Shore streams in the spring. These fish migrate to the lake very soon after stocking (Close et al. 1989). A weight of 5 g was used for all chinook salmon smolts, regardless of prior stocking size.

Weights at each age are needed for bioenergetics modeling, but often only lengths were reported in the literature. Length-weight relationships were calculated from available data, or obtained from other sources, for use when weights were not reported. Sizes of chinook salmon and length-weight relationships varied greatly between Lake Superior and other lakes (MNDNR, file data; Stewart et al. 1981; Halseth et al. 1990). However, the length-weight relationships of chinook salmon within Lake Superior appeared to be similar (Figure B2).

A collection of chinook salmon scales is housed at the Duluth Area Fisheries office of the MNDNR, but little analysis had been completed prior to this study. Mean lengths at age of spawners, and back-calculated lengths at age were available from a few Minnesota fish (Table B3). Scales from spawning chinook salmon, however, are poorly suited for back-calculation because of considerable erosion and resorption of the scale margin.

Spawning chinook salmon which returned to the French River trap from 1986 to 1989 had a mean length of 836 mm, and mean weight of 6,548 g, and all fish were assumed to be age 4 (D. Schliep, MDNR, personal communication), although they ranged from age 3 to age 5. Lengths, weights, and ages of creeled chinook salmon were available for Michigan waters of Lake Superior (Michigan Department of Natural Resources, Marquette Fisheries Station, unpublished data; Table B3). Weight values from the various sources varied (Table B3), but intermediate values were selected for use in bioenergetics simulations (Table B7). The maximum weight attained in simulations was 7,000 g.

Diet.--Diet of chinook salmon varied among Minnesota's Lake Superior management zones (Conner 1991), but the food habits within Minnesota waters as a whole were used in simulations of all life stages of chinook salmon. Data for fish less than 130 g were unavailable. Diet was grouped into the same five categories as for lake trout (Table C2), and the same caloric densities were used (Table C3).

Mortality.--Stocking records of fry and fingerling chinook salmon planted in North Shore streams in the spring provided initial population estimates (Table D1). A mean of 464,316 chinook salmon fingerlings were stocked annually from 1986 to 1989; fry stocking was discontinued after 1987. Chinook salmon return to their stocking streams as adults to spawn and die. The number of adults returning to spawn in the French River is known, but all fish were assumed to be age 4 (D. Schliep, MDNR, personal communication), precluding the calculation of total mortality for each year-class. Annual mortality rates have also not been calculated for Minnesota chinook salmon.

Simulations of Minnesota chinook salmon (Table D3) used mortality rates similar to those of Lake Michigan chinook salmon (Stewart et al. 1981), but mortality rates of young-of-the-year (YOY) were increased to account for a lower availability of food, and lifespan was increased because of the higher spawning age. Simulations of chinook salmon included 5 year-classes (age 0 to age 4), and assumed increased mortality at age 3 and older to account for spawning (Table D3).

Spawning.--Chinook salmon enter Minnesota's North Shore streams to spawn in late October. Most spawn at age 4, but some age 3, and fewer age 5 also spawn (Negus et al. 1990). Recent scale readings indicate that more age 5 spawners return to the French River than previously believed (D. Schliep, MDNR, personal communication), so future simulations should include age 5.

Coho salmon

Temperature.--Literature references for coho salmon temperature preference in Lake Superior were not found. Sources (Table A4) suggested that coho salmon prefer warmer temperatures than lake trout or chinook salmon, and coho salmon in Lake Superior are reported to inhabit water closer to the surface than other salmonines (J. Selgeby, National Fisheries Research Center, personal communication). Winter temperatures in Minnesota waters of Lake Superior are fairly uniform, but summer surface temperatures may reach 12°C to 16.8°C (Close et al. 1984). The winter temperature regime for coho salmon simulations was the same as for lake trout and chinook salmon (dropping to 1.1°C), but summer temperatures were warmer (up to 14.0°C) than for other salmonines (Table A7).

Age and Growth.--Coho salmon are not currently stocked in Minnesota waters, but juveniles (age 1) and adults migrate to Minnesota waters to feed. Hassinger (1974) reported a mean length of 318 mm during their first summer in the lake, and a mean length of 528 mm during their second summer, for coho salmon originally stocked as yearlings. Some scales have been collected from creeled coho salmon in Minnesota, but age and growth determinations have not been completed in recent years. The most comprehensive growth data found was from Michigan waters of Lake Superior (Table B4), and these compared well with Hassinger's (1974) data. The length-weight relationships for coho salmon in Minnesota and Michigan waters were similar (Figure B3), based on creeled fish. A smolt weight of 32 g (Becker 1983), and weights from Michigan fish (Table B4) were used in coho salmon simulations (Table B7). The maximum weight attained in simulations was 1,362 g, which is equal to the weight of Michigan coho salmon in November.

Diet.--Coho salmon diet varied by management zone (Conner 1991), but data from Minnesota waters as a whole were used in simulations of all life stages of coho salmon. Data for coho salmon less than 160 g were unavailable. The diet was divided into the same five categories with the same caloric densities as that of lake trout (Tables C2 and C3).

Mortality.--Coho salmon smolt in spring as yearlings, and some migrate to Minnesota waters to feed. After about 17 months in the lake, they migrate back to their natal streams to spawn and die. The mean annual harvest of coho salmon in Minnesota's sport fishery from 1984-1988 was 4,077 (Hansen 1990). The harvests in 1983 and 1989 were higher, so the overall mean harvest is approximately 5,000 (Morse 1990). Based on a light exploitation rate (approximately 10%), the total population of catchable size (age 2) coho salmon in Minnesota waters of Lake Superior was estimated at 50,000 fish. Population abundances used in coho salmon simulations are given in Table D2, and a 50% annual mortality rate was estimated (Table D3).

Spawning.--Coho salmon are presently stocked only in Michigan waters of Lake Superior, but they reproduce naturally in other parts of Lake Superior and stray extensively (Hansen 1990). Coho salmon enter tributaries to spawn from September to March of their second year of lake life, but most spawn in October (Hansen 1990). Little spawning occurs in Minnesota streams. Simulations in this study ended on 1 November of the second lake year, corresponding with their migration away from Minnesota waters.

Steelhead

Temperature.--Reported temperature preferences for rainbow trout ranged from 5°C to 20°C depending on life stage and location (Table A5), but most temperatures were higher than those reported for lake trout and chinook salmon. Summer temperatures used in simulations reached a high of 13.0°C, and were intermediate between those of chinook salmon and coho salmon; winter temperatures were the same for all species modeled, dropping to 1.1°C in March (Table A7).

Age and Growth.--Steelhead are stocked as unfed swim-up fry in Minnesota's North Shore streams. Some age 0 parr are apparently displaced into Lake Superior during spates (MDNR, unpublished data). Age 2 and age 3 steelhead were captured in the French River smolt trap in spring 1990; these fish were most likely smolts, but some parr marks were still visible. Juveniles moving downstream were therefore termed "emigrants," with no distinctions implied regarding smoltification. The allocation of stocked fish into each life history category for modeling is explained in Table D3.

Size at age of steelhead depends on the number of years spent in a stream and the number of years spent in the lake. Ages were reported in "stream years/lake years" format, which is more informative than total age. Aging and back-calculation of scales from spawning, creeled, and smolting steelhead is in progress at the Duluth Area Fisheries office of the MDNR, and the completed portion of this information was used in this study (Table B5). These recent data indicate some size differences from those reported by Hassinger et al. (1974). Back-calculated lengths at annulus formation were reported by Scholl et al. (1979; Table B5) for steelhead in the Brule River, Wisconsin, but these fish were more robust than Minnesota fish (Figure B4). Wild steelhead populations in Lake Superior exhibit significant genetic differentiation between different drainages (Kreuger and May 1987), which emphasizes the importance of local data.

Weights were often unreported in the literature, so weights were estimated from length-weight relationships. A length-weight relationship was developed for steelhead using data from spawning fish returning to the French River and Knife River in spring 1990, and from age 1 parr in the Split Rock River in spring 1990 (Figure B4). Weights of emigrating steelhead were estimated from fish captured in a smolt trap in French River. Data in Table B5 were used to estimate weight at age for older cohorts in bioenergetics simulations (Table B7).

When actual weights from young steelhead were input into the bioenergetics model, the maximum ration (P value = 1.0) was exceeded. Decreasing the weight inputs for younger fish enabled ration levels to stay below maximum, and weights at later ages were increased to make up the difference (Table B7). The maximum weight attained in simulations was 3,200 g.

Diet.--The diet of rainbow trout varies with season and the changing availability of insect prey (Table C2). Data for fish less than 350 g in Lake Superior were unavailable. Winter dietary proportions were estimated, assuming a lower utilization of insects resulting from their reduced availability during that season (Conner 1991). Caloric densities of diet items are listed in Table C3.

Mortality.--Data from an auger smolt trap in the French River in 1990 suggest that approximately 918 age 0 fish, or 0.4% of the 233,720 fry stocked in the French River emigrated to Lake Superior in their first year. The mortality of age 0 emigrants is extremely high (Hassinger et al. 1974). Close (in review) reported parr mortality rates ranging from 84% to 98% during their first summer in the stream (Table D3). Hassinger et al. (1974) reported 94% mortality for juveniles to age 2 or age 3 smolts (Table D3). These mortality rates during the stream phase of life, along with stocking records (Table D1), were used to calculate the number of steelhead entering the lake. Bioenergetics simulations of steelhead in Lake Superior began with these population estimates, and covered the lake phase of their life. A mean of 2,350,317 steelhead fry were stocked annually into North Shore streams from 1983 to 1989 (Table D1).

Mortality estimates have not been calculated for the lake phase of steelhead life in Minnesota waters since Hassinger et al. (1974), and ages of returning spawners appear to have increased since that time. Kwain (1981) reported a 41% annual mortality rate for steelhead returning to Stokely Creek in eastern Lake Superior. Swanson (1985) reported mortality rates in Pikes Creek, Wisconsin ranging from approximately 50% to 66% for age 3 to age 6 fish, and 80% to 100% for older fish. Mortality rates used in simulations were intermediate between these reported values (Table D3).

The combined mortality estimates of Close (in review), Hassinger et al. (1974), Kwain (1981), and Swanson (1985) which were used to simulate Minnesota fish, were similar to the lifetime mortality rates of Pikes Creek steelhead (Swanson 1985), although they were calculated over somewhat different intervals. The mortality of steelhead in Pikes Creek from eggs to age 1 was 99%, and the mortality from age 1 to spawning was 95%. These rates were similar to those used in this study (Table D3), where the mortality from fry stocking to emigration at age 2 or 3 was 99% (the combination of 90% mortality during the first summer, followed by 94% mortality from fall to emigration), and mortalities from stream emigration to age 2/3, 2/4, 2/5, and 3/3 were 91%, 96%, 98%, and 88%.

Mortality from eggs to maiden spawners in Pikes Creek was >99%. Mortality of stocked fry to age 2/3 (the age of most French River spawners) was >99%. Inclusion of age 0 emigrants in these calculations would increase mortality rates.

Spawning.--Steelhead ascend Minnesota's North Shore streams to spawn from about mid-April to mid-May, depending on latitude and temperature. Steelhead may spawn more than once, but mortality increases at spawning time due to angler harvest, stress, and injury.

The age of spawning depends upon life history strategy. Hassinger et al. (1974) reported that 75% of the 1961-1965 spawning runs in Kadunce and Kimball creeks consisted of age 2/2, 2/3, 3/2, and 3/3 fish, with a 23% contribution from age 1/2, 1/3, 2/1, 2/4, and 3/1 fish. The 1990 spawning runs in the French and Knife rivers were primarily (82%) age 2/3, 2/4, 2/5, and 3/3, and only 13% were age 2/2, 3/2, 3/4, and 3/5. For model simulations, I assumed that spawning began in the third lake year on 1 May.

The proportion of weight lost during spawning was measured for female steelhead in the Brule River, Wisconsin (Scholl et al. 1984). Females in the size range corresponding to those returning to the French and Knife Rivers (in Minnesota) lost a mean of 14.7% of their body weight during spawning. Weight loss for male steelhead was not measured, but male lake trout lose about 1.4% of their body weight during spawning (Stewart et al. 1983). Simulation models require data representative of the average individual, which accounts for males, females, and non-spawners, so the proportion of weight lost during spawning was estimated at 7%.

Kamloops

Temperature.--Temperature preferences of Kamloops and steelhead were assumed to be identical. No additional information was found.

Age and Growth.--Kamloops with clips identifying year-class, and weighing approximately 100 g, are stocked into the lower ends of North Shore streams as presmolt yearlings, about 1 June. These fish leave the streams soon after stocking. Fin-clipped yearlings weighing approximately 300 g are imprinted to French River water, and stocked into Minnesota waters of Lake Superior about 1 October (Table D1). Kamloops fry were stocked into some tributary steams of management zone MN-3 before 1989.

Kamloops returning to the French River to spawn in 1990 were measured and aged by fin clip (Table B6). Back-calculations of sizes at younger ages were unavailable. Kamloops up to age 9 were caught in the French River from 1977 to 1987, but the majority returned at ages 4 or 5 (MDNR, file data). Kamloops ages are reported in total years in this study.

Spawning Kamloops have a length-weight relationship similar to that of spawning steelhead (Figure B5). Weights of age 3 to age 5 Kamloops reported in Table B6 provided a basis for weights used in simulations (Table B7); weights of aged fish were not routinely recorded prior to 1989. The weight of age 2 Kamloops was estimated from steelhead weights, since weights for age 2 Kamloops were unavailable. Weights of Kamloops age 6 and older were estimated from the larger fish in the 1990 spawning run, since weights of older Kamloops were not available. Kamloops stocked as fry were assumed to smolt at age 2, at weights identical to the spring stocked yearlings. The maximum weight attained in simulations was 3,700 g.

Diet.--Food habits of Kamloops and steelhead were assumed to be identical.

Mortality.--Mortality rates for Kamloops in Minnesota waters have not been reported in the past, so estimates were made. Kamloops fry were assumed to have an instream mortality rate similar to steelhead fry (Table D3). Kamloops are particularly vulnerable to predation when they first enter Lake Superior, and mortality rates were assumed to be high in their first lake year. Kamloops staging near river mouths for about six months prior to spawning are subject to high fishing pressure. Stress and injury during spawning also contribute to mortality (Table D3). A mean of 483,224 Kamloops (fry, spring yearlings, and fall yearlings) were stocked annually from 1983 to 1989; fry stocking was discontinued after 1988 (Table D1). Although the numbers and ages of spawning adults are recorded annually in the French River, the incidence of repeat spawning is unknown, so total mortality for each year-class could only be estimated.

Spawning.--Kamloops enter streams to spawn in early spring, and may spawn more than once in their lifetime. Kamloops enter streams a few days earlier than steelhead, but often do not ascend as far. Reports from anglers and other agencies suggest that some Kamloops stray from their stream of stocking; spawning fish with Minnesota fin clips have been captured in Wisconsin and Michigan streams. Spawning occurs from ages 2 to 9, but most spawning occurs at ages 4 and 5. Kamloops may spawn more than once. The proportion of weight lost during spawning is assumed to be similar for Kamloops and steelhead.

Atlantic salmon

Temperature.--Temperature preferences of Atlantic salmon in Lake Superior have not been reported. Preferences in other lakes varied from 12°C to 20°C, depending on locality (Table A6). Atlantic salmon in Lake Superior were assumed to occupy temperatures similar to chinook salmon, ranging from a low of 1.1°C in winter to 12.0°c in summer (Table A7).

Age and Growth.--Atlantic salmon are stocked into Minnesota's North Shore streams as fry, or into river mouths near Lake Superior as fingerlings and yearlings. Fry are stocked about 1 May, fingerlings about 1 October, and yearlings about 1 June (Table D1). Fingerlings and yearlings enter Lake Superior soon after stocking. Atlantic salmon smolts (originally stocked as fry) were captured in the French River in May and June 1990. Eight sampled fish were all age 2. I used total ages for Atlantic salmon in this paper, because of the varied life histories, and the lack of age and growth information.

Length-weight relationships of Atlantic salmon from Minnesota and Maine were similar (Figure B6), but growth rates were very different (Table B6). Length was greater at each age in Minnesota, although measurements were taken in fall rather than at annulus formation.

Weights used in Atlantic salmon simulations were reduced from those in Table B6 to approximate weight at annulus formation (Table B7). The maximum weight attained in simulations was 2,800 g. Age determinations were completed on only 20 spawning fish from 1988 and 1989, and no creeled fish, at the time of this study. Back-calculations of sizes at younger ages were not done. Most spawning Atlantic salmon that returned to the French River in 1988 and 1989 were age 4, with some age 3 and age 5.

Diet.--Diet of Atlantic salmon in Minnesota waters of Lake Superior consisted mainly of rainbow smelt (Table C2). Data for fish less than 1,020 g were unavailable, but food habits were assumed to be similar for all cohorts. Winter dietary proportions were estimated, assuming a lower utilization of insects and crustaceans resulting from their reduced availability during that season (Conner 1991). The caloric densities of diet items are listed in Table C3.

Mortality.--Sixty-eight smolts (primarily age 2) were captured in the French River smolt trap in spring 1990. The trap efficiency was approximately 6.1%, so a total of about 1,115 smolts, or 1.9% of the fry stocked in 1988, survived. This survival may be unusually low considering the severe 1989-1990 winter conditions in North Shore streams, so the average mortality rate of fry to smolt was estimated at 96% (Table D3).

Mortality rates for Atlantic salmon in Lake Superior have not been calculated. Mortality of fingerlings and yearlings entering Lake Superior was assumed to be high, with lower rates at later ages, similar to those of steelhead and Kamloops. Mortality was high at spawning time due to stress, injury, and angling. A mean of 105,007 Atlantic salmon (fry, fingerlings, and yearlings) were stocked annually into Minnesota waters from 1984 to 1989; fry stocking was discontinued after 1988 (Table D1). Total numbers of spawning adults returning to the French River are recorded annually, but total mortalities for each age-class could only be estimated due to the lack of age and repeat-spawning data (Table D3).

Spawning.--Atlantic salmon enter Minnesota's North Shore streams to spawn about 15 October. Ages were determined for 20 of the 37 spawning fish returning to the French River in 1988 and 1989: 5% were age 3, 75% were age 4, and 20% were age 5. Spawning Atlantic salmon in Maine rivers range from age 3 to 10 (Havey and Warner 1970). Atlantic salmon may spawn more than once in their lifetime, but repeat spawning is low.

The weight lost during spawning was measured for female Atlantic salmon of Ungava Bay in eastern Canada (Power 1969). Females similar in size to those returning to the French River lost a mean of 4% of their weight during spawning. Weight loss for male Atlantic salmon was unavailable, but was assumed to be similar to lake trout; approximately 1.4% (Stewart et al. 1983). Simulation models require data representative of the average individual, which accounts for males, females, and nonspawners, so the proportion of weight lost during spawning was estimated at 2%.

Sea lamprey

Temperature.--The optimal temperature range for growth of sea lamprey is 15°C to 20°C. Growth is intermediate at 10°C, and low at 4°C (Farmer et al. 1977). Sea lamprey are subject to the temperature preferences of their hosts, which were assumed to be lake trout in this study (Table A7). Thus temperatures occupied in Minnesota waters (1.1°C to 10.0°C) are conducive to slow or intermediate growth.

Age and Growth.--Sea lamprey ammocoetes may remain in streams for 6-8 yr, with some reports of up to 15 yr (Beamish 1980; Becker 1983). Larvae transform and migrate downstream to the lake from September to May. Sea lamprey parasitize fish for 12-20 months before their spring spawning migration. Sea Lamprey enter Lake Superior at approximately 4 g, and grow to about 200 g during their parasitic phase (J. Heinrich, U.S. Fish and Wildlife Service, Sea Lamprey Control Station, personal communication).

Diet.--Large lake trout appear to be the preferred prey of sea lamprey (Johnson and Anderson 1980). Lake trout blood has an energy density of 765 cal/g wet weight, and sea lamprey tissue has an energy density of 1,224 cal/g wet weight (Kitchell and Breck 1980). Predator energy density, as well as prey energy density, is required in the sea lamprey bioenergetics model.

Mortality.--Most sea lamprey in Minnesota waters of Lake Superior have migrated from spawning streams in other states and Canada. They return to their natal streams to spawn and die (Becker 1983). Estimates of sea lamprey abundance in other parts of Lake Superior have been based on counts of spawning adults in streams, but abundance and wounding rates in Minnesota waters are disproportional to the amount of spawning habitat. Abundance estimates in Minnesota waters range from 5,000 to 10,000, with an annual mortality rate during their parasitic phase of 5% (M. Ebener, Great Lakes Indian Fish and Wildlife Commission, personal communication). Simulations of sea lamprey began with 8,170 lamprey at the start of lake life on 1 October, declining to 7,500 at the end of their second lake year.

Spawning.--North Shore streams are generally unsuitable for lamprey reproduction due to migration barriers and inadequate substrate. Spawning occurs in spring, and feeding ceases prior to spawning. All lamprey die following spawning.

Forage species

Forage fish in Lake Superior are subject to predation pressure by other fish, and harvest by commercial fishermen. Salmonines in Lake Superior utilize insects and crustaceans in their diet to varying extents, but fish are the primary forage (Tables C1 and C2). Rainbow smelt and coregonines, especially lake herring and chubs (bloater plus kiyi), are most widely utilized as forage in Minnesota waters. Rainbow smelt, lake herring, and chubs comprise the bulk of the commercial fishery in the Minnesota waters of Lake Superior (Schreiner and Morse 1990). From 1985 to 1989, the commercial harvest of rainbow smelt fluctuated between 64.0 and 127.6 metric tonnes, the harvest of chubs fluctuated between 1.4 and 4.1 metric tonnes, and the harvest of lake herring increased from 25.0 to 103.5 metric tonnes.

Forage fish populations are sampled annually by the U.S. Fish and Wildlife Service - National Fisheries Research Center, Ashland Biological Station, Wisconsin. Samples are collected during May-June with a bottom trawl. Tows are made perpendicular to shore, between the 15 m to 70 m depth contours. Ten stations are sampled annually in Minnesota waters. Lake herring larger than 250 mm were rarely captured in Minnesota waters, but lake herring of that size were also rarely found in predator stomachs. These forage fish samples have traditionally been used to compare relative abundance between years, rather than to calculate biomass.

Bathymetric distribution studies using bottom trawls (National Fisheries Research Center, Ashland, unpublished data) show that 69.6% of rainbow smelt were found in between the 15-70 m contours, for the entire lake across all years. The bathymetric distribution of lake herring, based on average spring catch in gill nets (set on the bottom) from 1958-74, indicated 69.4% were between the 15-70 m contours. Bathymetric distribution of lake herring was not sampled with trawls. The bathymetric distribution of bloaters, based on average spring catch in bottom trawls from 1958-74, indicated 46.5% were between the 15-70 m contours.

Biomass estimates for this study have all been based on bottom sampling, and distributions higher in the water column are unknown. Total spring biomass for each species was determined by multiplying the average catch per hectare by 26,235 hectares (the surface area of Minnesota waters between the 15 m and 70 m contours), and dividing the result by the proportion of the population found between the 15-70 m depth contours (Table G1). Argyle (1982) found that 22% of the smelt in Lake Huron in spring were not near the bottom and were therefore unavailable to trawls. Similar data from Lake Superior were unavailable, but considering that lake herring are often well above the bottom and are also found in lake depths greater than 70 m, biomass estimates of lake herring are probably greatly underestimated.

Theoretically, the total biomass of forage fish existing in Minnesota waters of Lake Superior in one year includes the biomass at the time of spring sampling plus the biomass produced during the year. Production of each year-class and species can be calculated using the equation, $P=N_2W_2-N_2W_1+(N_1-N_2)(W_2-W_1)/2$, where N_1 = population number at the time of sampling in one year, N_2 = population number in the next year, W_1 = mean weight of individual fish in the first year, and W_2 = mean weight of individual fish in the next year (National Fisheries Research Center, Ashland, unpublished data). The equation assumes a linear rate of increase in mean body weight and a decline in population abundance. The information needed to calculate this equation has been collected by the National Fisheries Research Center, but production of forage species in Minnesota waters has not been calculated in recent years.

A production:mean biomass ($P/\bar{B}$) ratio of 1.11 was calculated for rainbow smelt in U. S. waters of Lake Superior, 1978-1981 (National Fisheries Research Center, Ashland, unpublished data). $P/\bar{B}$ ratios have not been calculated for lake herring or bloaters, but may be approximately 0.6 - 0.7. Production was estimated using these ratios, and added to the total biomass to determine the approximate amount of forage fish available within one year (Table G1).

Bioenergetics Methods

Model Simulations

The Generalized Bioenergetics Model of Fish Growth (Hewett and Johnson 1987) was used to model consumption based on growth of the major salmonines in Minnesota waters of Lake Superior. Data gathered for the model included: 1) dates of stocking into the streams or lake, and dates when smolts enter the lake; 2) numbers of fish stocked and numbers of smolts entering the lake; 3) mortality rates in each year of life; 4) growth (weight) in each year of life in the lake; 5) temperatures occupied during the year; 6) food habits, and percentage of each diet item consumed, preferably during each season and life stage; 7) caloric density (calories/g wet weight) of each diet item, and (for the sea lamprey model only) caloric density of the predator; 8) percentage of indigestible material in each diet item; 9) proportion of total body weight lost in spawning; and 10) date and age of spawning.

Population estimates and model simulations of chinook salmon, steelhead, Kamloops, and Atlantic salmon were based only on stocked fish. Stocked lake trout were modeled separately from native lake trout, and all modeling of coho salmon was based on naturalized fish. Sea lamprey were modeled on the assumption that their energy consumed represented "lost growth" of salmonines, which in turn represents forage consumed.

Simulations were run only for the lake resident portion of each species' lifespan, and most were run with 1 June as simulation day 1 and 31 May as simulation day 365. Most species entered the lake as smolts or were stocked about 1 June, and thus their predatory impact began on that date. Exceptions were age 0 native lake trout which begin to feed approximately 1 July, lake trout fingerlings which were stocked in late October, and some Kamloops yearlings and Atlantic salmon fingerlings which were stocked approximately 1 October. Each of these exceptions was modeled from their respective simulation day to 31 May. Coho salmon leave Lake Superior to spawn approximately 1 November in their second lake year, and their simulation was terminated on that date.

The bioenergetics program contains models and associated parameters for lake trout, chinook/coho salmon, and sea lamprey. The chinook/coho salmon model contains several physiological parameters derived from rainbow trout (Stewart and Ibarra, in press), and is the most appropriate model currently available for both rainbow trout and Atlantic salmon. However, the intercept for the maximum consumption function is somewhat inappropriate for these species (D. Stewart, State University of New York, personal communication), and simulations of steelhead and Kamloops did not permit the input of observed growth in the first two lake years. The consumption rate (P) needed to accommodate the growth rate of young steelhead and Kamloops exceeded 1.0 (theoretical maximum ration), because of the low caloric density of their insect diet. Consequently, weight inputs had to be reduced for the first two years of the simulations, and increased in later years (Table B7). A rainbow trout model is currently being developed by P. Rand and D. Stewart at the State University of New York in Syracuse.

All stocked lake trout were modeled in one simulation, with spring stocked yearlings joining fall stocked fingerlings on 1 June. Stocked lake trout were modeled separately from native lake trout, to account for their different life histories, weights in the first seven years, and mortality rates in the first five years (Tables B7 and D3). Temperature, diet, and spawning were modeled the same for native and stocked lake trout.

All chinook salmon were modeled in the same simulation, assuming fingerlings and presmolts entered the lake at the same date and size. Steelhead were modeled in three simulations, based on one, two, or three years of stream life prior to lake life, with appropriately adjusted mortality rates and sizes at smolting. The distribution of stocked steelhead fry into each of these life history strategies is explained in Table D3. All Kamloops were modeled in the same simulation, with spring yearlings and age 2 smolts beginning on 1 June, and fall stocked yearlings joining the others on 1 October. Atlantic salmon were modeled in three simulations, based on stocking size as fry (into streams), fingerlings, or yearlings. Sizes and mortality rates were adjusted accordingly.

Bioenergetics models typically represent the average individual of a species, but groups of individuals can be modeled by adding population estimates and mortalities. Simulations can be used to determine consumption by all existing year-classes simultaneously within a single year (a population "snapshot"), or they can be used to determine the consumption by one group of fish over several years (a year-class "biography"). Consumption can be totaled for each year, or cumulative consumption can be totaled over many year-classes. I used each of these scenarios to examine various aspects of the salmonine predatory impact in Minnesota waters of Lake Superior:

1) *Baseline data.*--The preliminary modeling effort was aimed at using the most complete and current data available (Tables A7, B7, C1, C2, C3, D3) to estimate cumulative consumption by all major salmonines in Minnesota waters of Lake Superior within one year, simultaneously (the "snapshot" approach). These simulations represent all year-classes extant in 1989, the most recent year with completed records of spawning returns and some fish ages.

The influence of sea lamprey on salmonines was investigated in additional simulations. Sea lamprey affect salmonine populations by causing increased mortality and decreased growth, and were modeled because of their indirect impact on the forage base. The total mortality rates used in all salmonine simulations included mortality due to lamprey predation, but impacts on consumption were addressed separately. Two year-classes of sea lamprey were simulated assuming a lake trout diet, and lake trout temperature regime. The output from the simulation (grams of lake trout consumed) was added to the production of age 7 lake trout, and the lake trout simulation was redone to determine the theoretical amount of forage consumed by sea lamprey via lake trout.

2) *Species-specific predatory impacts.*--Simulations of each species, starting with hypothetical stockings of 100,000 fish, were used to determine the relative predatory impact of each species. These simulations followed each group of stocked fish through each year in its lifespan (the "biography" approach; this would be the same as a "snapshot" of the population, if 100,000 fish had been stocked annually). Cumulative consumption was totaled for the lifespan of each stocking group. Unlike the baseline simulations, this scenario eliminated the effect of varied stocking levels, and demonstrated how all the other variables associated with each species influenced forage consumption. Populations stocked into streams were reduced by appropriate mortality rates (Table D3) before they entered the lake. Temperatures, growth, diets, and mortality rates were consistent with baseline data.

3) *Distribution of predation over time.*--Total consumption during each year was calculated to track consumption by each year-class of each species. This scenario demonstrated how declining population abundance and increasing growth rate exert a combined effect on consumption. Simulations began with 100,000 fish of each species at each stocking size, and the age of greatest predatory impact was determined. Temperatures, growth, diets, and mortality rates were consistent with baseline data.

4) *Predatory impacts of individual fish.*--Individual fish from each species and stock-

ing size were modeled for a simulated lifetime, to compare their relative consumption of forage fish. Simulating the consumption by one fish eliminated the influence of mortality rates encountered in previous simulations. Cumulative consumption at each age was calculated. The relative "costs," in terms of forage, of individuals at equal size or lifestage were compared. Temperatures, diets, and growth were consistent with baseline data.

5) *Predator growth as an indication of prey availability.*--The bioenergetics model was used to simulate growth at given levels of consumption, rather than to simulate consumption at known growth rates. Lake trout and chinook salmon growth were simulated using different levels of consumption, to mimic changes in prey availability. The P value in the bioenergetics model represents the proportion of maximum ration actually consumed by the fish, based on current temperature and fish size, and can be related to prey availability. Baseline P values (determined for fish sampled in 1989; Table H1) were increased or decreased by 0.1 (10% of the maximum ration) to simulate the growth of each year-class under conditions of increased or decreased prey availability.

Simulations of each year-class were run beginning with baseline starting weights, plus increased or decreased rations, to determine changes in final weight after one year. Additional simulations were run over multiple year-classes, using the final weight achieved in each year as the starting weight for the next year, to determine the changes in growth after several years of increased or decreased ration. Rainbow trout and Atlantic salmon simulations were not run, because their simulations utilized the chinook/coho model with a maximum consumption intercept less suited to other species.

Sensitivity Analysis

Sensitivity analyses similar to those of Kitchell et al. (1977) and Stewart et al. (1983) were performed on the model variables, which require data specific to each population. Model parameters (included in the consumption models, respiration models, and egestion/excretion models) were not changed. I simulated consumption by one individual of each species using baseline data. I then repeated each simulation, modifying one variable at a time by increments of + or - 10%, to demonstrate the effects of modifications in each variable. Variables that did not lend themselves to 10% modifications were incremented appropriately, e.g. spawning was either present or absent. All diets were reduced to one item, rainbow smelt, to simplify comparison of total consumption.

Sensitivity analyses were performed on populations of lake trout and chinook salmon, to evaluate the effects of input variations over multiple year-classes. Simulations of more than one fish also permitted evaluation of changes in mortality rates, age of first spawning, and growth distribution between years. Mortality was incremented + or - 10% of the numerical value; for example, if the baseline mortality was 89%, simulations were run at mortalities of 89 + 8.9 = 97.9% and 89 - 8.9 = 80.1%. When the addition of 10% to the mortality exceeded 100%, the simulation was terminated with that year-class. Fifteen year-classes of lake trout and 5 year-classes of chinook salmon were modeled, beginning with populations of 500,000 fish.

Bioenergetics Results

Model Simulations

Baseline data.--The estimated amount of forage fish consumed in 1989 (Table F1) plus the amount harvested commercially greatly exceeded the estimate of total forage fish biomass plus production (Table G1). Consumed and harvested rainbow smelt totaled approximately 2,900 metric tonnes, while initial biomass plus production was about 185 metric tonnes. Consumed and harvested coregonines totaled approximately

350 metric tonnes, while initial biomass plus production was about 62 metric tonnes.

Simulations of all year-classes extant in 1989 revealed that lake trout (stocked and native) were responsible for 56.7% of the consumption of rainbow smelt and 83.1% of the consumption of coregonines (Table F1). Chinook salmon consumed 25.8% of the rainbow smelt and 6.5% of the coregonines. Coho salmon consumed 8.2% of the rainbow smelt, and 9.1% of the coregonines. Consumption of rainbow smelt and coregonines by all other species was 9.4% and 1.4% of the total consumption (Table F1).

Kamloops were responsible for 51.4% of the consumption of insects, lake trout consumed 21.0%, steelhead consumed 11.2%, coho salmon consumed 8.4%, chinook salmon consumed 7.8%, and Atlantic salmon consumed 0.2% (Table F1). Lake trout were responsible for 55.3% of the consumption of crustaceans, chinook salmon consumed 31.8%, coho salmon consumed 10.6%, and Atlantic salmon consumed 2.1% (Table F1).

Sea lamprey simulations yielded a consumption estimate of 6.554 x 10^6 g of salmonine prey. Adding this biomass to lake trout production demonstrated the indirect impact of sea lamprey on forage fish. Lake trout consumption of rainbow smelt increased by 1.19% (1.7 x 10^7g), coregonines by 1.28% (2.4 x 10^6g), insects by 0.84% (1.0 x 10^6g), crustaceans by 0.17% (2.0 x 10^5g), and other fish by 1.14% (1.4 x 10^6g). Mortality caused by sea lamprey is a separate effect, and was included in total mortality estimates for lake trout.

Species-specific predatory impacts.--Consumption estimates were highly dependent upon mortality rates of each species, so the populations having the lowest mortality rates were responsible for the highest consumption (Tables D3 and F2). Lake trout stocked as spring yearlings, with their relatively low mortality rates and long lives, consumed the most forage fish. Fish stocked as yearlings were generally responsible for the greatest consumption of rainbow smelt and coregonines. Chinook salmon (stocked as fry and fingerlings) were the exception, consuming the second highest amount, because they spend little time in streams, grow rapidly, and require many calories. Other species stocked as fry and fingerlings undergo high mortality during the stream phase of their life, and subsequent consumption of forage in the lake is relatively low.

Distribution of predation over time.--The age at which each species exerts the greatest influence on the forage base is shown in Table F3. Consumption is greatest during the year following the formation of the annulus ("age") given. Predatory impacts of Kamloops and Atlantic salmon yearlings are greatest in the first year after stocking. Atlantic salmon fingerlings show their greatest impact during the second year after stocking, and chinook during the third year after stocking. Steelhead and Kamloops fry have their greatest impact during the fourth year after stocking; lake trout yearlings have the greatest impact during the sixth year, and fingerlings during the seventh year, after stocking.

Relative predatory impacts of individual fish.--Cumulative consumption of forage fish by one predator fish of each species and stocking size is given in Table F4. Weights of consumed rainbow smelt and coregonines were totaled for comparative purposes. Stocking size generally had little effect on cumulative consumption compared to the species effect.

Chinook salmon are apparently the most efficient at converting forage fish to growth. A 3,000 g (age 3) chinook salmon has consumed 10,472 g of forage fish, a 3,000 g (age 5) Atlantic salmon has consumed over 17,076 g of forage fish, and a 3,000 g (age 12) lake trout has consumed about 26,000 g of forage fish. A 3,000 g steelhead or Kamloops has consumed about the same amount of forage fish as a chinook salmon, but their growth is slower, and their diets include a greater percentage of insects and crustaceans (Tables C1 and C2).

However, chinook salmon also consume the greatest quantity of forage fish per unit time, and the typical spawning chinook salmon caught by anglers has "cost" far more, in terms of forage, than other species (Table F4). A spawning coho salmon, steelhead (age 2/3), Kamloops (age 4 or 5), or Atlantic salmon (age 2/2) has consumed only 10-30% of the forage fish consumed by a spawning chinook salmon (age 4). Lake trout between ages 6 and 9 (the ages most caught by anglers; Morse 1989) have consumed only 23-41% of the forage fish consumed by spawning chinook salmon (age 4).

Predator growth as an indication of prey availability.--Weight at age attained by lake trout utilizing several simulated prey availabilities is shown in Figure H1. Weight at age attained by chinook salmon utilizing several simulated prey availabilities is shown in Figure H2. Mean weights for fish in each year-class in 1989 are shown in the baseline data lines. Baseline growth is the weight difference between successive years. Weight attained after one year of increased or decreased ration should be compared to baseline weight in the preceding year to determine growth for that year. Growth achieved while utilizing increased or decreased rations over all years can be calculated by comparing weights in successive years at that ration.

Increased ration caused lake trout and chinook salmon growth to increase, and decreased ration caused growth to decrease relative to baseline levels. One year of reduced ration caused lake trout to gain little or no weight at several ages (or sizes), and even caused weight loss at some ages (or sizes). Reduced ration over many years provided only enough energy for maintenance of lake trout, with little or no surplus for growth. Reduced ration over one or many years provided sufficient energy for chinook salmon growth at every age.

Sensitivity Analysis

Single fish sensitivity analyses (Table E1) gave results similar to whole population sensitivity analyses. Sensitivities determined from simulations of one age 7 lake trout were within 1% of those determined from simulations of an entire lake trout population, for changes in prey caloric density, indigestible fraction, temperatures, weights (increased only), and proportion of weight lost during spawning (Table E1). Ten percent reductions of all weights of the lake trout population caused cumulative consumption to decrease 9.1%, compared to a 6.8% consumption decrease for the single fish. Raising the population's spawning age by one year caused cumulative consumption to decrease 1.4%, and lowering the spawning age one year caused cumulative consumption to increase 2.1%. Increasing all mortality rates of the population by 10% caused cumulative consumption to decrease 12.0%, and decreasing all mortality rates by 10% caused consumption to increase 14.7%. Increasing the growth of age 2 lake trout by 10%, and reducing the subsequent growth of age 3 lake trout, caused cumulative consumption to increase 0.5%.

Sensitivities determined from simulations of one age 3 chinook salmon were within 1% of the sensitivities determined from simulations of an entire chinook population, for changes in prey caloric density, indigestible fraction, temperatures, and weights (decreased only)(Table E1). Ten percent increases in all weights of the population caused cumulative consumption to increase 11.1%, compared to a 12.2% consumption increase for the single fish. Increasing all mortality rates of the chinook salmon population by 10% (and raising the age 4 annual mortality rate from 99% to 100%) caused cumulative consumption to decrease 46.3%, and decreasing all mortality rates by 10% caused consumption to increase 60.8%.

Discussion

Data Compilation

Temperature.--Temperature selection by an individual fish appears to be influenced by available temperature, preferred temperature, and acclimation temperature (Neill and Magnuson 1974; Stewart 1980). Food availability, predator or competitor avoidance, light intensity, dissolved oxygen, season, strain of species and geographical location also may affect temperature selection (Magnuson et al. 1979; Stewart 1980; Negus et al. 1987). Beitinger and Magnuson (1975) suggest that lake trout will occupy the warmest available temperature up to but not exceeding their preferred temperature. Field observations of lake trout, however, suggest that they normally occupy a temperature at least 2°C lower than the laboratory determined preferendum (Ferguson 1958; Elrod and Schneider 1987).

Age and Growth.--The bioenergetics model requires input of weights at known ages, and these data were unavailable for some Minnesota salmonines, particularly at the juvenile stage. The length-weight relationships for chinook salmon, steelhead, Kamloops, and Atlantic salmon (Figures B2, B4, B5, and B6) were derived from spawning fish, and may be less accurate for younger fish. Weights from spawning fish were not consistently recorded until recently. Data obtained from creel surveys were usually lacking weight or age information. Weights attained by salmonines are dependent upon temperature and forage, which vary between different locations in Lake Superior. Some species appear to have similar length-weight relationships regardless of location, but sizes at age may vary considerably. If we are going to use and develop better energetics models in the future, collection of weight data should be routine.

Diet.--The diet information in this report was obtained primarily from fish captured by anglers and charter boat operators. Diet may vary further offshore, so information from the mid-lake is needed. Diet information for small fish in Minnesota waters was available only for lake trout. Winter diet information was also limited, but this information is important because piscivory may increase in winter following declines in insect and crustacean prey. The diets of chinook salmon and coho salmon appear to vary depending on management zone (Conner 1991), so collections should be made from multiple locations.

Diet data are often poorly suited for use in bioenergetics modeling. Dietary input should be in the form of percentage by weight of diet items. Percentage by volume is roughly equivalent to percentage by weight for aquatic organisms, and is recommended when weight cannot be readily measured. Diet information reported as percent occurrence is difficult to use; each prey type can be converted to weight if the number of items is known, but this approach is tedious.

Caloric densities of many prey items were not readily available, and the bioenergetics model is particularly sensitive to changes in energy density of prey (Beauchamp et al. 1989). The wide range of energy densities reported for invertebrate and fish species creates a potential for significant variation in estimated consumption, if caloric data from one species is substituted for another (Beauchamp et al. 1989). Caloric densities of some species also change with the season. Inaccuracies in dietary rations of high calorie items create greater errors in consumption estimates. Lack of data on lake herring, opossum shrimp, and other fish in this study may have contributed to some inaccuracy.

Food habits of salmonines may reflect changes in rainbow smelt and coregonine populations. Periodic assessment of diet information is needed to determine the impact of each predator species on the forage base, particularly if forage stocks are in danger of overexploitation. If predator stocks switch to heavy utilization of recovering lake herring stocks, that prey species may be threatened once again. Diet information may be obsolete in less than 5 years.

Mortality.--Mortality rates in Minnesota waters have only been calculated for lake trout. The number of smolts produced from fish stocked into streams is largely unknown, although steelhead smolt abundance has been estimated in the past, and is currently being researched. Mortality estimates of lake fish are confounded by repeat spawning, inadequate age information, and the difficulty of obtaining mortality rates of juvenile fish. Simulation results were sensitive to variation in mortality rates, so increased emphasis on determination of mortality rates is warranted.

The contribution of naturally reproduced salmonines other than lake trout is unknown. This study indicated that the dynamics of all species must be understood for effective management to occur.

Spawning.--Data on numbers and sizes of spawning chinook salmon, steelhead, and Kamloops have been obtained using the French River and Knife River traps. These traps offer the potential to gather additional information such as numbers of repeat spawners, percentage of weight lost during spawning, annual mortality rate, and growth, which is needed to develop realistic bioenergetic simulations.

Forage species.--The forage fish sampling done by the National Fisheries Research Center has provided valuable data for assessing relative abundance and comparing relative densities between species (Hansen 1990). However, I have shown that biomass estimates derived from those data are almost certainly underestimates. Given the biomass estimates, no reasonable level of production could support the commercial fishery and estimated predation pressure. I suggest that the most critical information need is for reliable forage biomass estimates, accounting for midwater fish.

Rainbow smelt and lake herring populations in Lake Superior have been relatively unstable over the past 30 years (Hansen 1990). Since many of the predator species currently rely on stocking to sustain their populations, fisheries managers are in a position of control over predatory impacts. The very fact that prey populations are unstable emphasizes their vulnerability to overexploitation, and increases the need to assess stocking plans bioenergetically.

Stewart et al. (1981) warned of the danger of overstocking salmonine predators, which were found in Lake Michigan to consume alewives (and other prey) at rates more proportional to their own than to alewife densities. A weak year-class of prey fish would then be subjected to intense predation pressure, which could amplify prey population cycles and result in a catastrophic decline in stocks. A rapid switch to other forage species could similarly depress the other forage populations before any management action based on stocking rates could be effective (Stewart et al. 1981). This warning should be heeded in Minnesota waters of Lake Superior, where predator stocking is high, rainbow smelt populations are rapidly declining, and high hopes are set on the recovery of lake herring stocks.

Model Simulations

Baseline data, and species-specific predatory impacts.--Lake trout, chinook salmon, and coho salmon are responsible for consuming the greatest portion of forage fish in Minnesota waters of Lake Superior. Stocking of lake trout and chinook salmon could be modified to alter predation pressure. Since coho salmon have become naturalized, controlling their numbers would be much more difficult.

The preference for low temperature, lower and slower individual consumption of forage fish, slow growth, and slow response to fluctuations in the forage base are indications that lake trout is a species naturally adapted to the cold and unproductive waters of Lake Superior. Chinook salmon, which consume large amounts in a short time, could be formidable competitors if forage fish are limiting. Atlantic salmon, also highly piscivorous, is another potential predator. However, the future of Atlantic salmon in Minnesota waters is dubious, due to their low survival, and the possible cessation of stocking. Potential for competition is also posed by coho salmon, steelhead, and Kamloops. The actual presence of competition may only be confirmed by demonstrating a limiting forage base.

Although indirect forage consumption by sea lamprey was relatively low, there may be more subtle affects on consumption. The energy density of host blood declines during the sea lamprey attack (Cochran and Kitchell 1989), but these simulations did not reflect a caloric decrease. Salmonines attacked by sea lamprey experience increased stress and infection (Kitchell and Breck 1980; Cochran and Kitchell 1989), which may affect their metabolism, food conversion efficiency, and activity. Basic model parameters may vary somewhat for parasitized fish. The insensitivity of the model to parameter errors (Kitchell et al. 1977; Stewart et al. 1983) should minimize the importance of these differences, however.

Lifetime consumption of a species per 100,000 stocked is presented in Table F2, assuming diets, mortality rates, temperatures, and growth rates remain at the levels determined for 1989. Consumption at other stocking levels could be predicted from this table if other variables remained unchanged.

Distribution of predation over time.--The consumption of forage fish over time varies greatly between species. Predatory inertia is a term applied to the time from stocking until the greatest predatory impact has occurred (Stewart 1980). The inertia for each species can be derived from Table F3 by determining the time from stocking of each size fish to the age at which greatest total consumption occurs.

Predatory inertia is a measurement of the time lag that typically occurs between any management action and the effect on a fish community. Predatory inertia indicates the suitability of a species for short-term management manipulations in response to forage fish fluctuations. Some species, such as Kamloops yearlings, have their greatest predatory impact when they are young due to their abundance. Others, such as lake trout, have their greatest impact at a higher age because the huge increase in individual consumption overshadows the decline in population up to that point.

Kamloops and Atlantic salmon yearlings have the least predatory inertia, but increased time in the hatchery makes them equivalent to Atlantic salmon fingerlings in terms of production for forage fish manipulations. Steelhead and Kamloops fry have a 4 year predatory inertia, but require very little hatchery expense. Steelhead and Kamloops consume more insects than fish (Table C2), however, making them less effective for forage fish manipulations.

Lake trout have the greatest predatory inertia of all salmonines stocked by Minnesota, and therefore have the least potential for short-term forage base manipulations. Lake trout currently exert the greatest impact on the forage base, since they have considerably longer lifespans than chinook salmon (Tables F3 and F4). Lake trout restoration was the original focus of Lake Superior rehabilitation efforts, and preserving lake trout stocks and forage remains a primary concern of managers and anglers. Manipulating the stocking quotas of other salmonine species should therefore be implemented to the advantage of lake trout (Busiahn 1990).

Chinook salmon have low predatory inertia (Table F3), are inexpensive, and consume a large amount of forage fish during their lake life (Table F4). Consumption of forage fish by chinook salmon is second only to consumption by lake trout. Manipulation of chinook salmon stocking quotas may be a particularly efficient way to manipulate forage abundance. If forage populations are depleted, a decrease in stocking quotas of chinook salmon could make a significant difference in a relatively short time.

Predator growth as an indication of prey availability.--The relationships between salmonine predators and their prey have been examined thus far by comparing the quantity of forage consumed to the quantity of forage available. An alternate approach is to examine the potential growth of salmonines under conditions of increased or decreased prey availability. Kitchell (1983) stated that the energy consumed by a fish is allocated in a hierarchical fashion, with metabolism, specific dynamic action, and waste losses taking precedence over growth. Surplus energy expressed as growth is thus the most variable component in the energy budget.

Figure H1 suggests that lake trout in the Minnesota waters of Lake Superior are living in a tenuous position, because decreases in prey availability could seriously affect growth. Reduced ration for even one year could result in little or no weight gain, so changes in mean weight at age could signal changes in prey availability. Figure H2 suggests that chinook salmon in Minnesota waters of Lake Superior are living well, with plenty of surplus energy for growth. If their ration is reduced, growth rate is only slowed. The change in growth rates between various rations is considerably less for chinook salmon than for lake trout.

Changes in relative abundance of rainbow smelt versus lake herring may also contribute to changes in growth of predator species. If rainbow smelt continue to decline and lake herring increase, salmonine predators may shift to utilize the most abundant prey. Differences in prey caloric density would alter the growth rates of fish utilizing the different prey.

Forage fish: consumption versus biomass discrepancy.--The poor correlation between predicted consumption and forage availability could be attributed to several factors: 1) inaccurate consumption estimates due to parameter errors in the bioenergetics model; 2) inaccurate prey caloric densities, incomplete diet information, inaccurate mortality or growth rates; 3) lack of knowledge about salmonine migration and consumption outside Minnesota waters; or 4) underestimated forage biomass. Some of these factors may be more significant than others.

The bioenergetics models have been found to be quite robust in spite of parameter changes, when used to predict consumption based on growth (Kitchell et al. 1977; Stewart et al. 1983; and Bartell et al. 1986). A model designed for largemouth bass *Micropterus salmoides* was verified when predicted consumption fell within 8.5% of measured consumption (Rice and Cochran 1984).

The quality of data used in this study influenced accuracy, but probably not enough to account for the forage base discrepancy. Prey caloric densities were similar to those used in other models, with fairly reliable results (Kitchell and Breck 1980; Stewart et al. 1983). Mortality rates, although not calculated from Minnesota stocks in every case, were similar to those calculated in other parts of Lake Superior (Table D3). Mean weights at each age may change as more accurate data become available, but the range of weights attained in the lifetime of the fish were based on reliable data. Variation of weight at each age had little affect on consumption estimates.

Minnesota's boundaries in Lake Superior are biologically arbitrary, as many of the anadromous species are known to stray or migrate across large portions of the lake. Forage in other parts of the lake may be utilized by fish stocked in Minnesota, but the reciprocal also may be true. The tradeoff of forage between different parts of the lake was assumed equal; consistent migration patterns for optimal foraging were considered unlikely with stocked fish.

Incomplete biomass estimates of forage fish are the most likely source of disagreement between consumption and availability. Sampling of rainbow smelt and coregonines with bottom trawls in Lake Superior is extremely difficult, due to lake size, depth, steep contours, gear biases, and distribution of the fish in the water column. The wide fluctuations exhibited in total biomass and mean size of the individuals sampled are evidence of these problems (Table G1).

Sensitivity Analysis

Bioenergetics models are composed of *parameters* consistent with the physiology of the modeled species, and *variables* consistent with the modeled population. Kitchell et al. (1977), Stewart et al. (1983), and Bartell et al. (1986) performed sensitivity analyses on bioenergetics models by varying parameter values. These sensitivity analyses verified the general robustness of the basic physiological components of the bioenergetics model, especially for estimating consumption based on growth. I tested the output sensitivity to input variable modifications rather than parameter modifications (Table E1). My analyses will be used to focus sampling efforts toward data requiring the greatest precision.

Changes in model outputs which are smaller than the ±10% input modifications suggest a low sensitivity. Outputs were least sensitive to the indigestible fraction of diet items, spawning weight loss, temperature, and spawning age (Table E1, and Sensitivity Analysis Results). Outputs were most sensitive to mortality rate, weight, and prey caloric density. These analyses tested the output sensitivity when all values for a particular variable were changed, and thus represent maximum output errors. Errors in individual data points for simulations of many year-classes would result in much smaller output errors.

Inclusion of more than one fish in a simulation results in a direct multiplication of predicted consumption, so a 10% modification in population abundance translates directly into a 10% change in output (consumption). Mortality rate modifications thus affect predicted consumption, but the output change depends on the age at which the mortality modification occurs. Modifications in mortality rates of young fish, which affect large numbers of individuals in all subsequent years, have more serious consequences than modifications in mortality rates of older fish. Overestimating the growth of younger cohorts in a population, and subsequently underestimating the growth of an older cohort causes a slight increase in total consumption, because more fish are affected by the growth increase in the younger year-class.

Information Needs

Improved estimates of forage fish biomass are essential for evaluating the significance of consumption estimates, and therefore supersede the data requirements for bioenergetics modeling. The information compiled for simulations of fish in Minnesota waters of Lake Superior revealed data shortages in several areas, and sensitivity analyses provided a means to identify and prioritize the information most critical to the accuracy of the bioenergetics models. The types of information needed, and some prospective data sources are outlined.

1) Computations of forage fish biomass are needed that account for fish at all depths and positions in the water column. Hydroacoustic sampling, in combination with the bottom trawls to estimate numbers of fish on the bottom unavailable to hydroacoustic gear, and midwater trawls to determine species composition, would provide a method to sample forage populations more accurately and extensively than methods used in the past.

2) An accurate computation of production by each species of forage fish is necessary to determine the amount available for consumption or harvest. Updated population assessments of forage fish could be used for these calculations. Production by year-class can be calculated, and updated P/B ratios developed.

3) Diet information from different size groups of each predator species, during each season, near shore and offshore should be updated about every five years, as the forage populations fluctuate. Accurate consumption estimates based on this diet information are essential to predicting impacts of each species on the forage base. Accuracy also depends on few "unidentified" items. Diet items must be reported as percentage by weight (preferably) or by volume. The Lake Superior Area of the MDNR is currently collecting diet information on lake trout as percent occurrence.

4) Determinations of caloric density are needed for each species identified in the diets of salmonines, especially lake herring and opossum shrimp.

5) Age and growth information is needed for each species of salmonine in Minnesota waters. Weights are particularly important for the bioenergetics model, and chang-

es in mean weight at age could be an indication of changes in prey abundance or species utilized. The Duluth Fisheries office of the MDNR has a large collection of scales from most salmonine species, and weight data are now being collected. Most scale samples have been taken from spawning fish, but scales of some creeled salmonines are available. Duluth Fisheries personnel are now aging spawning chinook salmon, steelhead, Kamloops, and Atlantic salmon (Spurrier 1991a, 1991b), and back-calculation of size at age will be done. The accuracy of back-calculations would be increased if scale samples from creeled and immature fish were used, since erosion and resorption of scales from spawning fish (especially chinook salmon) render them unreliable for back-calculations. Detailed age and growth information from both native and stocked lake trout is needed, and using polished otoliths would be most accurate for fish >age 7. Weisberg's (1987) growth model enables one to separate year effects from age effects on growth, and could be used to develop a biological chronology of growth so changes can be readily identified.

6) Mortality rates are needed for each species of salmonine in Minnesota waters at all life stages. Determining the smolt production for species stocked into streams is critical for beginning population estimates in the lake. A research project is underway at the Duluth MDNR to estimate smolt production indirectly by determining stream mortalities of juvenile steelhead. The proposed construction of weirs with smolt traps at the mouths of three streams may provide a means to sample anadromous species directly, and to determine the relationship between smolt production and adult survival.

The Duluth Fisheries office is tagging spawning steelhead and Kamloops to provide information on repeat spawning and mortality rates. Repeat spawning information also may be obtained from scale samples, at least for steelhead (Swanson 1985).

7) The extent of natural reproduction for each species of salmonine in Minnesota waters should be determined to increase the accuracy of abundance estimates. Natural reproduction of anadromous species is currently being monitored by electrofishing below the barriers of some North Shore streams (MDNR, stream assessments), but population estimates are not routinely done. A lakewide marking study, begun in 1988, will measure the extent of natural reproduction by chinook salmon. Natural reproduction of lake trout is monitored using egg traps and relative catches of clipped versus unclipped fish in gill nets (Schreiner et al. 1988, 1989, 1990).

8) Tagging studies to determine the extent of migration and straying are needed, especially if bioenergetics modeling is pursued for greater portions of Lake Superior. Feeding history may depend on location, since the relative abundances of forage species vary in different parts of the lake (Hansen 1990). Migrations also may affect temperatures occupied, survival,population estimates, growth rate, and strain encountered for each species.

9) Bioenergetics models developed specifically for rainbow trout and Atlantic salmon are needed for more accurate predictions of forage consumption. A rainbow trout model is currently being developed at the State University of New York in Syracuse by P. Rand and D. Stewart.

10) Temperatures occupied by each salmonine species in Minnesota waters of Lake Superior in each season are largely unreported. Collection of temperature data during routine lake trout assessment could improve the accuracy of lake trout simulations. Charter fishermen also may have some knowledge of temperatures occupied by salmonines in different seasons.

11) Bioenergetics models adapted for different life stages (especially juveniles) would improve accuracy, and might provide a means of predicting consumption, growth, and survival in the stream phases of anadromous species.

In summary, fisheries biologists from all agencies on Lake Superior should continue to work toward standardization of data collection, increased computerization, increased accessibility of basin-wide databases, and increased emphasis on multispecies management. Bioenergetics modeling of the species stocked by Minnesota is a step toward these objectives. It is hoped that this study will serve as a reference for continued modeling of fish stocks within Lake Superior, and contribute to future management strategies.

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APPENDIX A: Temperature Data.

Table A1.--Lake Superior water temperatures (°C), 18.3 m depth, at French River Coldwater Hatchery water intake, Duluth, Minnesota.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	**Annual Mean**
1980	4.1	2.6	1.6	2.3	4.2	6.8	10.2	9.4	10.9	9.7	6.1	4.1	6.0
1981	2.5	1.3	1.3	2.0	3.4	5.3	12.1	14.6	15.2	9.7	6.1	4.2	6.5
1982	2.3	1.1	0.8	1.7	3.2	6.7	10.6	9.3	11.9	10.7	6.3	3.8	5.7
1983	2.5	1.2	1.1	1.7	3.2	5.4	9.8	11.4	6.3	7.8	6.7	3.6	5.1
1984	2.6	1.3	1.0	1.4	3.0	5.4	8.3	13.1	9.4	8.3	5.3	4.1	5.3
1985	2.6	1.4	1.6	2.6	3.7	4.7	7.7	9.8	11.7	6.3	4.7	2.8	5.0
1986	1.7	0.4	0.5	1.6	3.1	5.1	9.8	10.3	11.1	10.0	4.1	2.6	5.0
1987	2.2	1.2	1.4	2.6	3.4	5.9	13.4	15.1	11.2	9.4	5.6	3.5	6.2
1988	1.9	1.2	0.6	1.6	2.7	5.2	9.5	12.9	9.9	8.4	5.1	3.2	5.2
1989	2.1	2.1	0.6	0.6	2.6	4.1	8.4	9.3	7.4	4.3	3.8	2.3	4.0
Monthly Mean	2.5	1.4	1.1	1.8	3.3	5.5	10.0	11.5	10.5	8.5	5.4	3.4	5.4

Table A2.--Lake trout *Salvelinus namaycush* temperature (°C) data.

Size or Age	Upper Avoidance	Final Preferendum or Temp. Occupied	Lower Avoidance	Location	Reference
YOY		5.6 - 17.2		Lake Superior	Becker 1983
YOY	15	7 - 14		Lake Superior	Peck 1982
YOY	17.2		5.6	Lake Superior	Wismer and Christie 1987
Young	14	11.5		Lab	Goddard et al. 1974
Young	15	11.7		Lab	McCauley and Tait 1970
Age 1-2	11.7		3.9	Lake Superior	Wismer and Christie 1987
Age 1-2	20	3.9 - 11.7		Lake Superior	Becker 1983
Age 1		7.5 - 10.3 (July-Oct.)		Lake Superior strain lake trout in Lake Ontario	Elrod and Schneider 1987
Age 2		3.9 - 9.5 (Apr.-Oct.)		Lake Superior strain lake trout in Lake Ontario	Elrod and Schneider 1987
Age 3		3.9 - 8.6 (Apr.-Oct.)		Lake Superior strain lake trout in Lake Ontario	Elrod and Schneider 1987
Age 4		3.7 - 6.5 (Apr.-Aug.)		Lake Superior strain lake trout in Lake Ontario	Elrod and Schneider 1987
Adult		11.8		Lake Michigan	Coutant 1977
Adult	18.3				Eddy and Underhill 1974
Spawning		7.8 - 11.1		Lake Superior	Becker 1983
(Feeding)		10.6			Becker 1983
(Unspecified)	18.3	10			Becker 1983

Table A3.--Chinook salmon *Oncorhynchus tshawytscha* temperature (°C) data.

Size or Age	Upper Avoidance	Final Preferendum or Temp. Occupied	Location	Reference
Small	25.1 (lethal)	11.7 - 15.5	Lab	Jobling 1981
470-950 mm TL, 1100-1230 g		6.5 - 13 (chinook and coho combined)	Lake Ontario	Haynes and Gerber 1989
Adult		17.3	Lake Michigan	Coutant 1977
(Unspecified)		6 - 8 (spring/summer)	North Pacific Ocean	Haynes and Gerber 1989
(Unspecified)		12 - 14		Scott and Crossman 1973

Table A4.--Coho salmon *Oncorhynchus kisutch* temperature (°C) data.

Size or Age	Upper Avoidance	Final Preferendum or Temp. Occupied	Lower Avoidance	Location	Reference
415-890 mm TL, 800-5900 g		6.5 - 13 (chinook and coho combined)		Lake Ontario	Haynes and Gerber 1989
Adult		16.6		Lake Michigan	Coutant 1977
Adult		11.4 (spring)		Lab	Coutant 1977
(Feeding)		12.2			Becker 1983
(Unspecified)		6.7 - 14.4			Becker 1983
(Unspecified)		8 - 12 (spring/summer)		North Pacific Ocean	Haynes and Gerber 1989
(Unspecified)		12 - 14			Scott and Crossman 1973
(Unspecified)	25	13 - 15			Jobling 1981
(Unspecified)		20		Lab	Wismer and Christie 1987
(Unspecified)	21	14.3 - 15.6	6	Lab	Cherry et al. 1982

Table A5.--Rainbow trout *Oncorhynchus mykiss* temperature (°C) data.

Size or Age	Upper Avoidance	Final Preferendum or Temp. Occupied	Lower Avoidance	Location	Reference
Fingerling	21	13 - 15		Lab	Talmage and Coutant 1980
Fingerling	22	18 - 19	14	Lab	McCauley and Pond 1971
150-250 g, Yearling		16.7		Lab	Wismer and Christie 1987
>1 Year		13			Kwain and McCauley 1978
Smolts		13.3 - 20	8.9	Brule River - Lake Superior	Niemuth 1970
Sub-adult and Adult		7.5 - 13.5		Lake Ontario	Haynes and Gerber 1989
Adult		13		Lab	Coutant 1977
Adult		16.5		Lake Michigan	Coutant 1977
Adult		11.3 - 14			Jobling 1981
Adult		11.6 - 15.8 (acclimation temps. 6 - 10)		Lab	Spotila et al. 1979
Adult		9 - 17		Lab	Wismer and Christie 1987
Adult		13		Lab	Garside and Tait 1958
Adult		16.5		Lake Michigan	Coutant 1977
Adult		15.6 - 21.1			Becker 1983
Spawning		5 - 13			Becker 1983
(Unspecified)	19	18	13	Lab	Cherry et al. 1975

Table A6.--Atlantic salmon *Salmo salar* temperature (°C) data.

Size or Age	Upper Avoidance	Final Preferendum or Temp. Occupied	Location	Reference
Young		14 - 16	Lab	Coutant 1977
(General)		12.1 - 15.1	Lab	Jobling 1981
(General)	14		Newfoundland Lakes	Leggett and Power 1969
(General)		<21 - 24	Maine Lakes	Havey and Warner 1970

Table A7.--Temperature (°C) inputs used in bioenergetics model simulations.

Month	Simulation Day	Lake trout	Chinook salmon	Coho salmon	Rainbow trout	Atlantic salmon	Sea lamprey
June	1	5.5	5.5	5.5	5.5	5.5	5.5
July	31	10.0	10.0	10.0	10.0	10.0	10.0
August	62	10.0	10.0	12.0	11.0	10.0	10.0
September	93	10.0	10.0	14.0	13.0	10.0	10.0
October	123	8.5	12.0	13.0	11.0	12.0	8.5
November	154	5.4	5.4	10.0	10.0	5.4	5.4
December	184	3.4	3.4	5.0	5.0	3.4	3.4
January	215	2.5	2.5	2.5	2.5	2.5	2.5
February	246	1.4	1.4	1.4	1.4	1.4	1.4
March	274	1.1	1.1	1.1	1.1	1.1	1.1
April	305	1.8	1.8	1.8	1.8	1.8	1.8
May	335	3.3	3.3	3.3	3.3	3.3	3.3
Annual Mean		5.2	5.5	6.6	6.3	5.5	5.2

APPENDIX B: Length and Weight Data.

Table B1.--Lake trout length (mm) and weight (g) data.

	Minnesota stocked lake trout[a] Small Mesh Gill Nets				Minnesota stocked lake trout[a] Large Mesh Gill Nets							
	August 1990		August 1989		May & Sept 1989		May 1988		May 1986		May 1985	
Age	Length	(Weight)	Length	(Weight)	Length	(Weight)	Length	(Weight)	Length	(Weight)	Length	(Weight)
1			198	(45)								
2	213	(82)	279	(186)								
3	307	(247)	287	(182)								
4	353	(373)	340	(313)					442	(638)	450	(842)
5	391	(485)	394	(477)	480	(912)	533	(1,262)	493	(948)	531	(1,354)
6	434	(649)	445	(745)	536	(1,320)	556	(1,453)	549	(1,401)	533	(1,369)
7			571	(808)	579	(1,708)	572	(1,598)	546	(1,374)	549	(1,490)
8					605	(1,979)	584	(1,710)	577	(1,675)	579	(1,736)
9					612	(2,056)	612	(1,999)	602	(1,958)	625	(2,162)
10					627	(2,230)	627	(2,166)	587	(1,787)	635	(2,262)
11					632	(2,290)	676	(2,782)	686	(3,146)	719	(3,231)
12					704	(3,285)	719	(3,415)				
13					721	(3,558)	747	(3,877)				
14					754	(4,132)						
15					739	(3,864)						

	Stocked lake trout[b], zone WI-2			Lake trout from zone MI-3[c]				Lake Michigan lake trout[d]
	Small Mesh Gill Nets	Large Mesh Gill Nets	Trawls	Stocked		Native		
Age	Length	Length	Length	Length	(Weight)	Length	(Weight)	(Weight)
1			130					(20)
2	221		203					(260)
3	282	345	257					(659)
4	340	472	300					(1,216)
5	396	511	328					(1,828)
6	470	551		566	(1,584)	528	(1,259)	(3,044)
7	541	582		592	(1,830)	561	(1,535)	(3,842)
8		632		605	(1,964)	605	(1,964)	(4,281)
9				635	(2,301)	658	(2,584)	(4,520)
10				673	(2,782)	686	(2,961)	
11				714	(3,374)	704	(3,222)	

[a] Stocked as fingerlings and yearlings, MN waters, Lake Superior. Small mesh net data from Schreiner (MN Dept. Nat. Res., personal communication); large mesh net data from Schreiner et al. (1988, 1989) and Spurrier and Morse (1985, 1986). Weights for fish in large mesh nets were estimated using Table B2.

[b] Stocked lake trout, Apostle Islands of Lake Superior, May 1962-1966 (Dryer and King 1968).

[c] Lengths from Lake Superior zone MI-3, 1980-89 (National Fisheries Research Center, Ashland, unpublished). Weights were estimated using the lakewide length-weight function (Figure B1).

[d] Weights from simulations (Stewart et al. 1983) based on data from Rybicki and Keller (1978).

Table B2.--Length-weight functions in Minnesota of stocked lake trout captured in large mesh gill nets, May and September, 1985-1989, in Minnesota waters of Lake Superior (S. Morse, MN Dept. Nat. Res., personal communication). W = Weight (g), L = Length (mm).

Year	Length-Weight Function
1985	$W = 0.2208((L/25.4)^{2.869})$
1986	$W = 0.0200((L/25.4)^{3.631})$
1987	$W = 0.1807((L/25.4)^{2.927})$
1988	$W = 0.0508((L/25.4)^{3.325})$
1989	$W = 0.0490((L/25.4)^{3.345})$

Table B3.--Chinook salmon length (mm) and weight (g) data.

Source	Age	Length	Weight
Negus et al. 1990[a,b]	1	287	158
	2	500	1,054
	3	692	3,209
	4	858	6,702
Minnesota Department of Natural Resources, file data[a,c]	2	828	5,933
	3	884	7,423
	4	964	9,988
Close et al. 1984[d]	1	250	98
	2	470	853
	3	640	2,456
J. Peck, Michigan Department of Natural Resources, Marquette, unpublished[e]	1	297	236
	2	457	763
	3	658	2,670
	4	798	4,690

[a] Chinook salmon stocked as pre-smolts for fluorescent pigment study in French River, MN.

[b] Back-calculated lengths at annulus formation. Weights were estimated using Figure B2.

[c] Mean lengths at capture of spawning chinook salmon in French River. Weights were estimated using Figure B2.

[d] Fall run chinook salmon stocked as pre-smolts in Minnesota streams. Mean lengths at annulus formation were back-calculated. Weights were estimated using Figure B2.

[e] Chinook salmon creeled near Marquette, MI, January-June, 1986-1987.

Table B4.--Mean lengths (mm) and weights (g) of age 2 coho salmon creeled in Lake Superior near Marquette, MI, 1985-1987 (J. Peck, Michigan Department of Natural Resources, Marquette, unpublished).

Month	Length	Weight
January	378	477
February	401	545
March	417	604
April	417	590
May	429	636
June	460	817
July	503	1,044
August	526	1,317
September	538	1,407
October	541	1,362
November	551	1,362
December	549	1,317

Table B5.--Steelhead length (mm) and weight (g) data.

Source	Stream years/ Lake years	Length	Weight
Minnesota Department of Natural Resources, file data, 1990[a]	1/5	701	2,043
	2/2	587	1,907
	2/3	632	2,315
	2/4	678	3,042
	2/5	683	2,951
	3/2	584	1,998
	3/3	655	2,769
	3/4	645	2,452
	3/5	668	2,860
Hassinger et al. 1974[b]	1/1	368	468
	1/2	457	883
	1/3	559	1,595
	1/4	617	2,131
	2/1	414	661
	2/2	528	1,349
	2/3	592	1,887
	2/4	678	2,809
	3/1	427	724
	3/2	556	1,570
	3/3	632	2,286
	3/4	660	2,596
Scholl et al. 1984[c]	1/2	467	1,148
	1/3	620	2,532
	1/4	671	3,156
	1/5	632	2,671
	1/6	686	3,357
	2/1	399	740
	2/2	541	1,731
	2/3	635	2,706
	2/4	668	3,117
	2/5	696	3,496
	2/6	711	3,710
	3/1	455	1,068
	3/2	574	2,042
	3/3	640	2,766
	3/4	676	3,222
	3/5	699	3,538

[a] Spawning steelhead from French and Knife Rivers, spring 1990.

[b] Spawning steelhead from Kadunce and Kimball Creeks, 1961-1965. Weights were estimated using Figure B4.

[c] Steelhead lengths at annulus formation, Brule River, Wisconsin, 1979. Weights were estimated from Figure B4.

Table B6.--Mean lengths (mm) and weights (g) of Kamloops and Atlantic salmon.

Source	Age	Length	Weight
	Kamloops		
Minnesota Department of Natural Resources, file data[a]	3	571	1,816
	4	625	2,410
	5	673	2,998
	6	661	2,919
	Atlantic salmon		
Minnesota Department of Natural Resources, file data[b]	3	546	1,290
	4	648	2,187
	5	689	2,643
	Landlocked Atlantic salmon		
Havey and Warner 1970[c]	3	230	
	4	373	
	5	419	
	6	467	
	7	505	

[a] Spawning fish, spring 1990, French River, Minnesota.

[b] Spawning fish, fall, 1988 and 1989, French River, Minnesota. Weights were estimated from Figure B6.

[c] fish from various lakes and rivers, Maine.

Table B7.--Weights (g) at each age used in simulations of salmonines and sea lamprey. All species were modeled starting on 1 June (simulation day 1) except where noted. Emigrants included smolts and displaced parr. Fgl = Fingerling, Yrl = Yearling, Emig = Emigrants.

	Lake trout		Chinook salmon	Coho salmon	Steelhead			Kamloops	Atlantic salmon		Sea lamprey
	Native	Stocked			Age 0 Emig	Age 2 Emig	Age 3 Emig		Age 2 Smolts	Stocked as Fgl or Yrl	
Age 0	0.5[a]	8[b]	5							8[g]	
Age 1	20	20[b],30[c]	177	32	20			100[e],300[f]		100[g],59[h]	
Age 2	70	82	1,000	817	450	30		600	28	1,000	
Age 3	200	247	3,000	1,362[d]	880	550	50	1,700	1,000	1,500	
Age 4	325	373	6,000		1,600	1,500	630	2,410	1,500	2,200	
Age 5	600	700	7,000		2,130	2,300	1,600	2,998	2,200	2,600	
Age 6	1,000	1,100			2,500	2,800	2,200	3,100	2,600	2,800	
Age 7	1,400	1,500			2,900	3,000	2,700	3,400			4[i]
Age 8	1,700	1,700			3,200	3,200	3,100	3,700			30
Age 9	2,000	2,000									200
Age 10	2,200	2,200									
Age 11	2,500	2,500									
Age 12	3,100	3,100									
Age 13	3,600	3,600									
Age 14	3,800	3,800									
Age 15	4,000	4,000									
Age 16	4,200	4,200									

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[a] Newly hatched lake trout, begin feeding about 1 July (simulation day 31).

[b] Originally stocked as age 0 fingerlings, about 28 October (simulation day 150).

[c] Stocked as yearlings, about 1 June.

[d] Weight at age 2 spawning, about 1 November (simulation day 154).

[e] Stocked as yearlings in several North Shore streams, about 1 June.

[f] Stocked as yearlings in French River, about 1 October (simulation day 123).

[g] Originally stocked as age 0 fingerlings in Lake Superior on about 1 October (simulation day 123).

[h] Stocked as yearlings into Lake Superior on about 1 June.

[i] Age when they enter the lake varies; larval phase in stream may last 6-8 yrs or more (Beamish 1980, Becker 1983); migration to lake occurs about 1 October (simulation day 123) through the following spring.

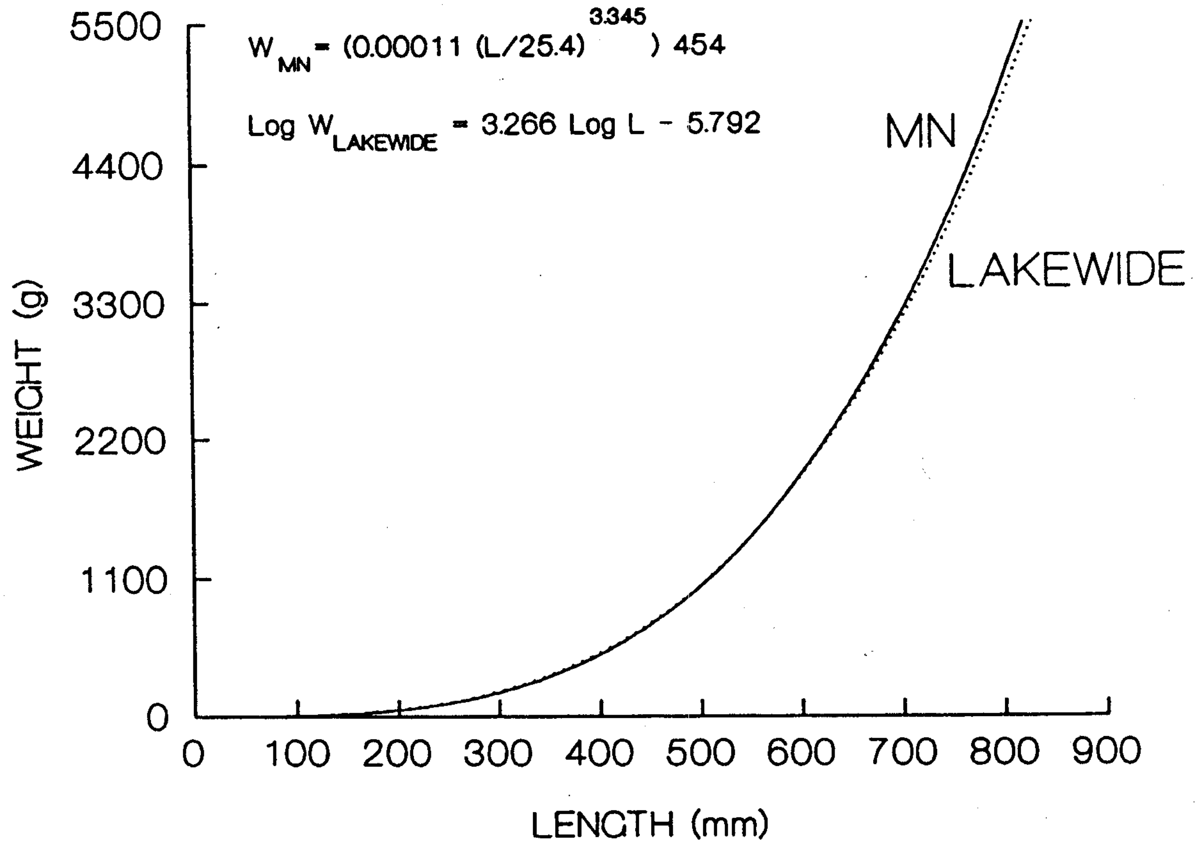

Figure B1.--Lake trout length-weight relationships. The Minnesota (MN) relationship was derived from stocked lake trout captured in large mesh gill nets, May and September, 1989 (Minnesota Department of Natural Resources, file data). The lakewide relationship was supplied by the National Fisheries Research Center, Ashland, Wisconsin. W = Weight (g), L = Length (mm).

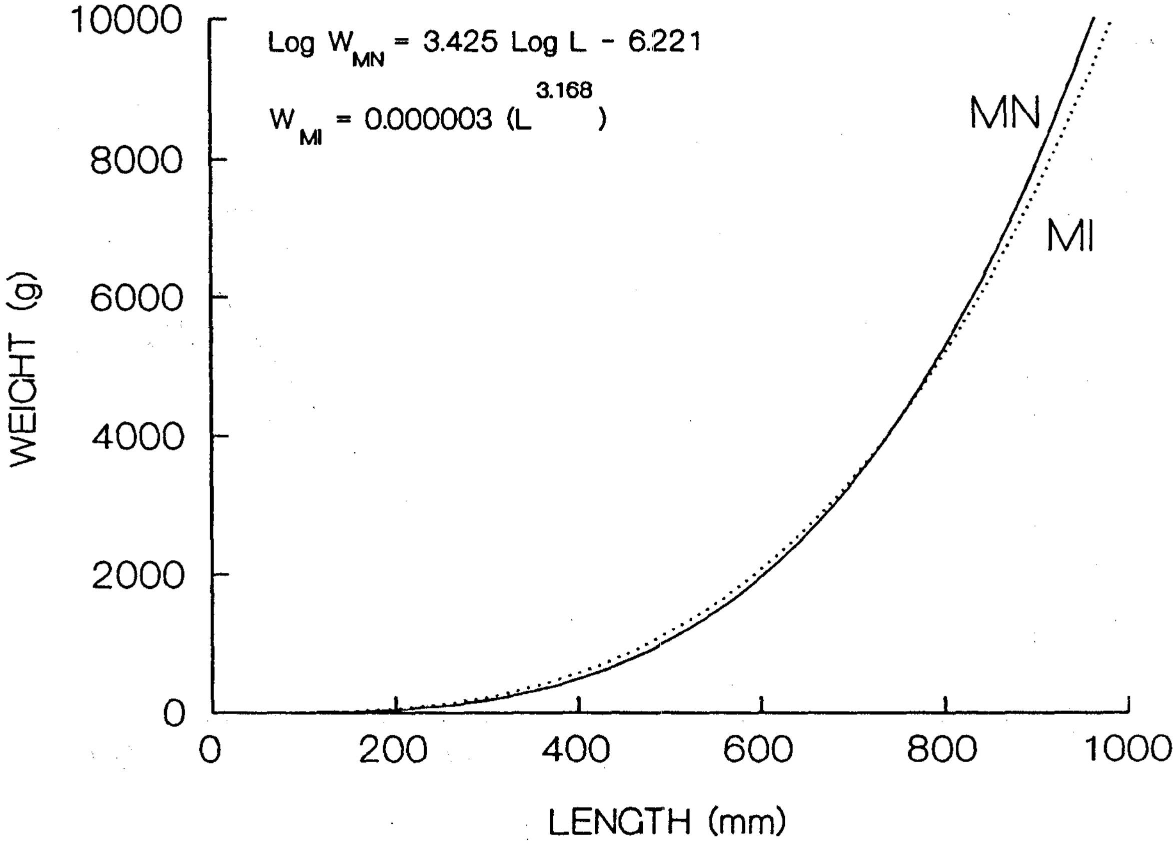

Figure B2.--Chinook salmon length-weight relationships. The Minnesota (MN) relationship was developed by Halseth et al. (1990) from spawning chinook salmon captured in October 1988. The Michigan (MI) relationship was derived from chinook salmon creeled in Lake Superior near Marquette, in January - June, 1986 and 1987 (Michigan Department of Natural Resources, Marquette, unpublished data). W = Weight (g), L = Length (mm).

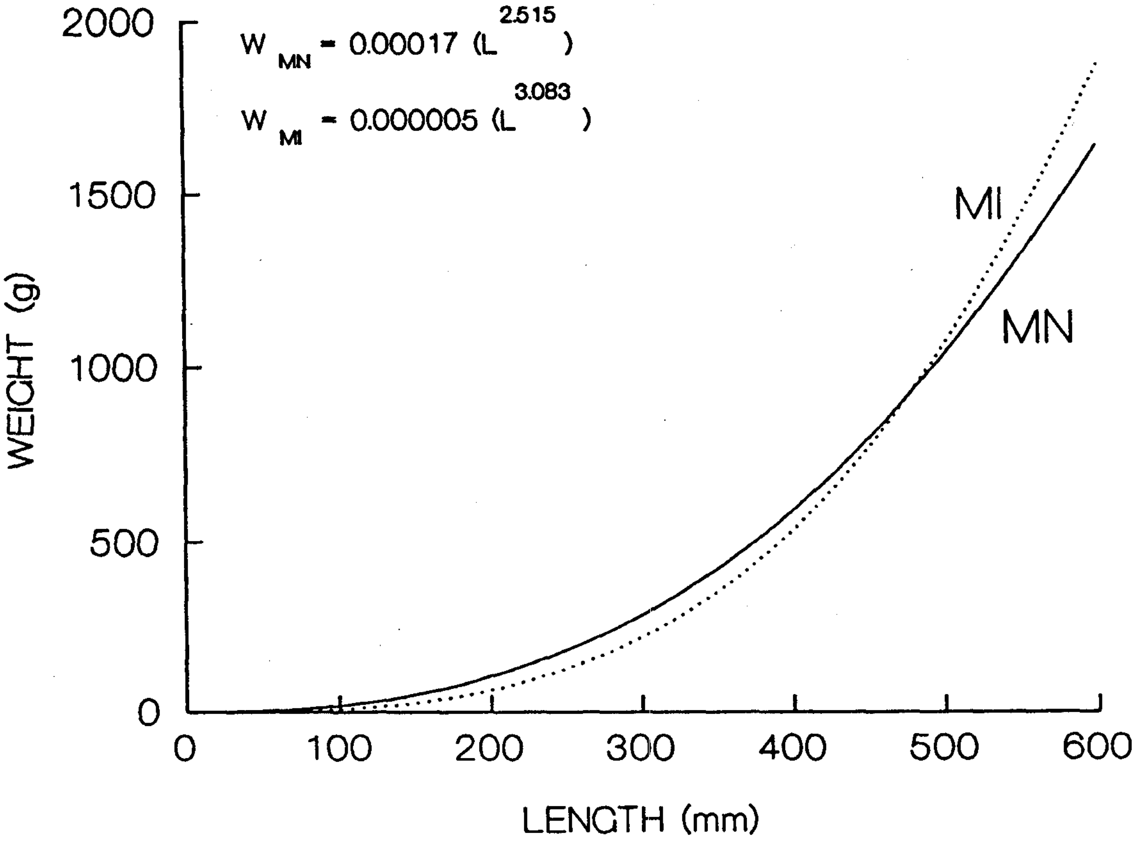

Figure B3.--Coho salmon length-weight relationships. The Minnesota (MN) relationship was derived from coho salmon caught in the 1989 and 1990 Beaver Bay-Silver Bay Lions Club fishing tournaments, the 1989 and 1990 Grand Slam Tournaments in Two Harbors, and the 1986 spawning coho salmon in the French River (Minnesota Department of Natural Resources, file data). The Michigan (MI) relationship was derived from coho salmon creeled in Lake Superior near Marquette, 1985-1987 (Michigan Department of Natural Resources, Marquette, unpublished data). W = Weight (g), L = Length (mm).

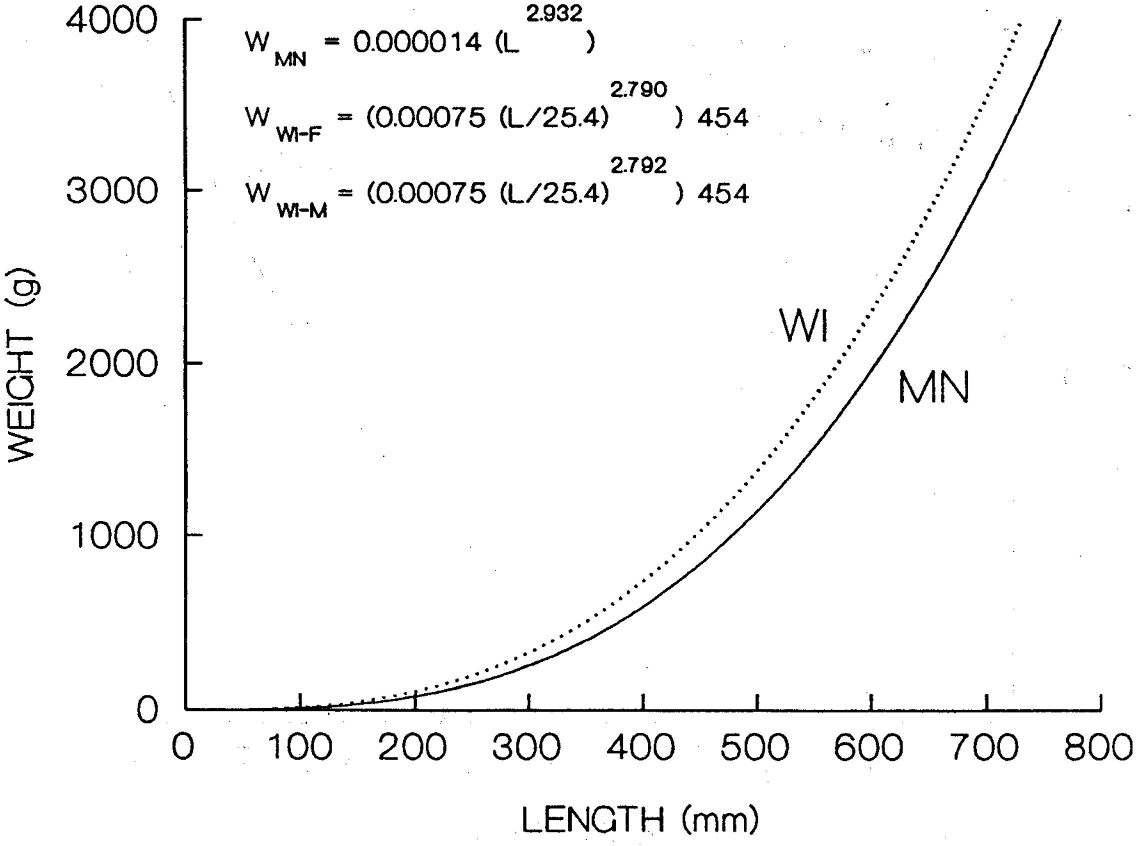

Figure B4.--Steelhead trout length-weight relationships. The Minnesota (MN) relationship was derived from spawning steelhead trout returning to the French and Knife Rivers in 1990, and age 1+ parr electrofished in the Stewart and Split Rock Rivers in 1989 (Minnesota Department of Natural Resources, file data). The Wisconsin relationships (virtually superimposed) were developed for male (WI-M) and female (WI-F) fish in the Brule River by Scholl et al. (1984). W = Weight (g), L = Length (mm).

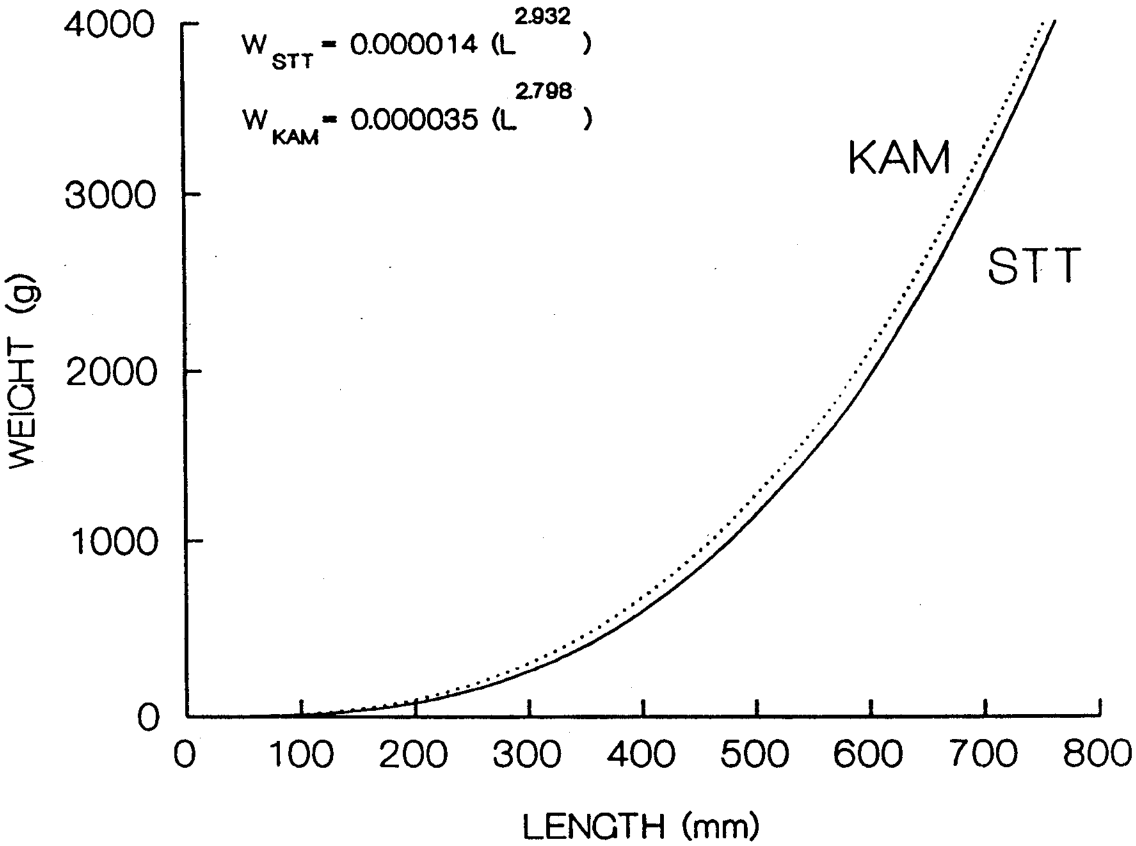

Figure B5.--Steelhead trout and Kamloops strain rainbow trout length-weight relationships. The steelhead trout (STT) relationship is identical to that in Figure B4. The Kamloops (KAM) relationship was derived from spawning fish returning to the French River in spring, 1990. W = Weight (g), L = Length (mm).

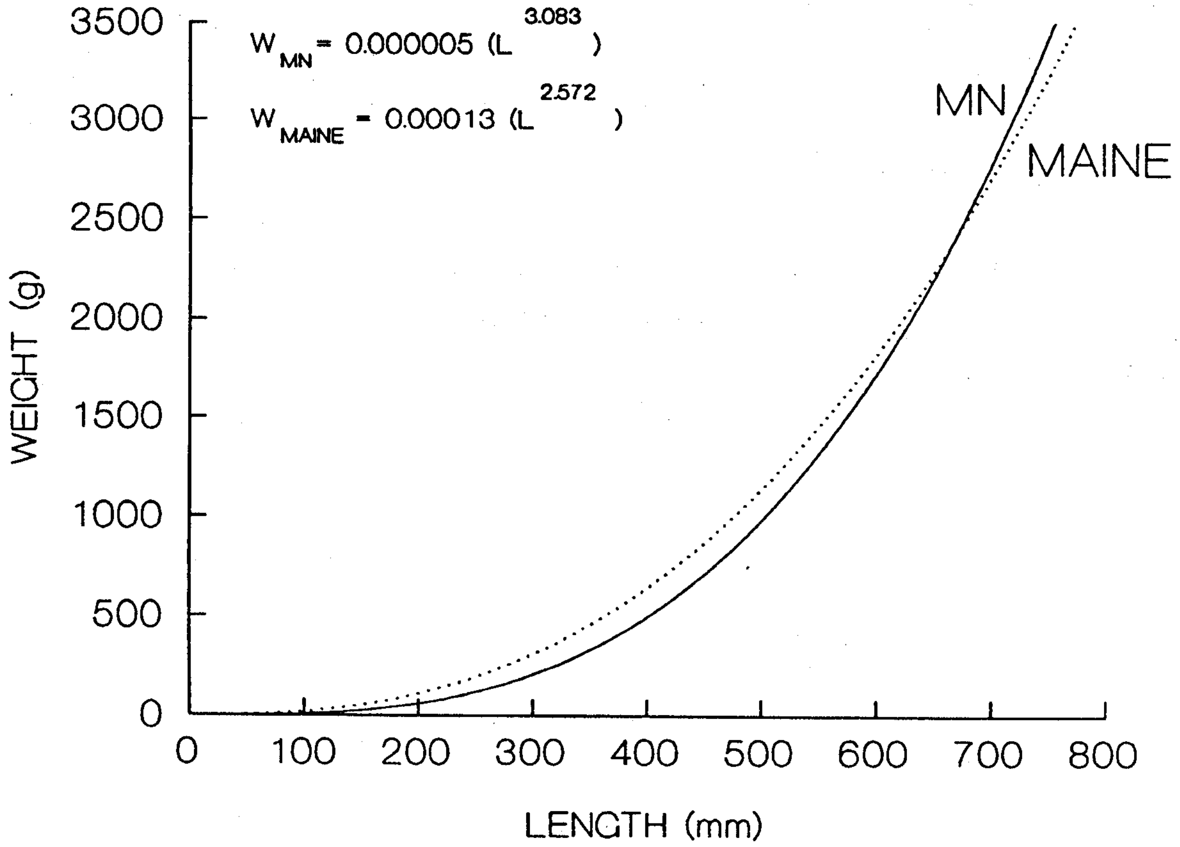

Figure B6.--Atlantic salmon length-weight relationships. The Minnesota (MN) relationship was derived from spawning Atlantic salmon returning to the French River in 1988 (Minnesota Department of Natural Resources, file data). The Maine relationship was derived from landlocked salmon in several Maine lakes and rivers (Havey and Warner 1970). W = Weight (g), L = Length (mm).

APPENDIX C: Diet and Prey Caloric Densities.

Table C1.--Seasonal proportions (% volume) of prey items in the diets of young-of-the-year lake trout (Swedberg and Peck 1984), yearling and age 2 lake trout (Anderson and Smith 1971; S. Morse, MN Dept. Nat. Res., personal communication, 1990), and all older cohorts in Minnesota waters of Lake Superior, 1984-1986 (Conner 1991). Values for days between dates were calculated in simulations by linear interpolation.

		Dietary proportion of				
Date	Simulation day	Rainbow smelt	Coregonines	Insects	Crustaceans	Other fish
			Young-of-the-year			
1 Jun	1	0.02	0.0	0.80	0.16	0.02
1 Oct	123	0.50	0.0	0.0	0.50	0.0
			Yearling			
1 Jun	1	0.04	0.0	0.24	0.70	0.02
1 Oct	123	0.50	0.0	0.0	0.50	0.0
			Age 2			
1 Jun	1	0.15	0.0	0.45	0.35	0.05
1 Oct	123	0.90	0.0	0.0	0.0	0.10
			Older cohorts			
1 Jun	1	0.78	0.03	0.11	0.03	0.05
1 Oct	123	0.89	0.10	0.01	0.0	0.0
1 Dec	184	0.55	0.45	0.0	0.0	0.0
1 Feb	246	0.60	0.01	0.0	0.01	0.38
1 May	335	0.78	0.03	0.11	0.03	0.05

Table C2.--Seasonal proportions (% volume) of prey items in the diets of chinook salmon, rainbow trout, coho salmon and Atlantic salmon in Minnesota waters of Lake Superior, 1984-1986 (Conner 1991). Winter diet of rainbow trout and Atlantic salmon is estimated, based on low availability of insects and crustaceans during winter months. Values for days between dates were calculated in simulations by linear interpolation.

		Dietary proportion of				
Date	Simulation day	Rainbow smelt	Coregonines	Insects	Crustaceans	Other fish
		Chinook salmon				
1 Jun	1	0.29	0.23	0.27	0.15	0.06
1 Jul	31	0.34	0.10	0.09	0.32	0.11
1 Aug	62	0.80	0.0	0.0	0.15	0.05
1 Sep	93	0.62	0.37	0.0	0.0	0.01
1 Nov	154	1.00	0.0	0.0	0.0	0.0
		Coho salmon				
1 Jun	1	0.06	0.0	0.75	0.18	0.01
1 Jul	31	0.09	0.01	0.62	0.24	0.04
1 Aug	62	0.18	0.39	0.08	0.32	0.03
1 Sep	93	0.45	0.05	0.0	0.0	0.50
1 Nov	154	1.00	0.0	0.0	0.0	0.0
1 Jan	215	0.84	0.0	0.15	0.01	0.0
1 May	334	0.60	0.0	0.39	0.01	0.0
		Rainbow trout				
1 Jun	1	0.02	0.0	0.98	0.0	0.0
1 Dec	184	0.50	0.0	0.50	0.0	0.0
1 Apr	305	0.02	0.0	0.98	0.0	0.0
		Atlantic salmon				
1 Jun	1	0.77	0.01	0.04	0.18	0.0
1 Oct	123	0.95	0.05	0.0	0.0	0.0

Table C3.--Caloric densities of the five diet categories used in simulations. Cal/g ww = calories per gram wet weight.

Organism	Cal/g ww	Reference
Rainbow smelt	1,590	Rottiers and Tucker 1982
Coregonines	2,360	Rottiers and Tucker 1982
Insects	759	Cummins and Wuycheck 1971
Crustaceans	1,058	Cummins and Wuycheck 1971
Small salmonines	1,295	Stewart et al. 1983

APPENDIX D: Population Abundances and Mortalities.

Table D1.--Numbers of salmonines stocked into Minnesota waters of Lake Superior or tributary streams, including year-classes extant in 1989 (Minnesota Department of Natural Resources, Annual Stocking Reports, 1975-1989). Abundance estimates are made for June 1, the starting date of the bioenergetics simulations. Fgl = Fingerling, Yrl = Yearling.

Year Stocked	Lake trout		Chinook salmon		Steelhead	Kamloops			Atlantic salmon		
	Fgl	Yrl	Fry	Fgl	Fry	Fry	Spring Yrl	Fall Yrl	Fry	Fgl	Yrl
1975		336,617									
1976		344,758									
1977		350,361									
1978		354,731									
1979		314,175									
1980		350,700									
1981	75,580	236,532									
1982	161,000	288,000			861,059						
1983		391,869			1,219,512	117,754	202,281	55,264			
1984	94,000	212,000			2,541,017	275,596	180,275	41,993	29,870	2,463	
1985	34,000	353,679	39,202	323,080	2,168,459	436,161	133,712	47,738	33,952		25,154
1986		408,215	64,719	526,536	2,514,071	644,384	91,178	70,120	25,513	13,407	28,634
1987		91,000	51,081	422,272	2,505,895	134,639	69,803	19,659	34,156		78,306
1988		211,000		390,135	3,603,275	453,909	126,446	46,497	60,291	112,927	42,500
1989	54,000	371,000		518,319	1,899,989		139,087	50,872		111,616	31,251
Mean (years)	46,509 (81-89)	307,642 (75-89)	51,671 (85-87)	464,316 (86-89)	2,350,317 (83-89)	343,741 (83-88)	141,140 (83-89)	47,449 (83-89)	36,756 (84-88)	112,272 (88-89)	41,169 85-89)

Table D2.--Estimated abundances in 1989 of native lake trout and naturalized coho salmon in Minnesota waters of Lake Superior. Abundance estimates are made for June 1, the starting date of the bioenergetics simulations.

Age	Lake Trout	Coho Salmon
0	1,107,770	125,000
1	114,100	62,500
2	36,860	
3	14,647	
4	31,664	
5	24,860	
6	8,740	
7	9,842	
8	2,096	
9	1,670	
10	551	
11	124	
12	133	
13	62	
14	49	
15	23	

Table D3.--Mortality rates used to calculate population numbers of salmonines in Minnesota waters of Lake Superior in 1989. Mortality rates are annual except where noted. Fgl = Fingerling, Yrl = Yearling, Emig = Emigrant.

	Lake trout[a]		Chinook salmon	Coho salmon	Steelhead			Kamloops	Atlantic salmon		
Age	Native	Stocked	Fry and Fgl	Naturalized	Age 0 Emig	Age 2 Emig	Age 3 Emig	Fry & Yrl	Fry	Fgl	Yrl
0		0.898[b]	0.80	0.50	0.90[c] 0.95[d]	0.90[c] 0.94[e]	0.90[c] 0.94[e]	0.99[f]	0.96[i]	0.95	
1	0.240	0.240	0.48	0.50	0.50			0.50[g] 0.80[h]		0.50	0.90
2	0.120	0.120	0.50		0.50	0.65		0.60	0.60	0.50	0.50
3	0.120	0.120	0.70		0.50	0.50	0.50	0.60	0.50	0.50	0.80
4	0.120	0.142	0.99		0.50	0.50	0.50	0.60	0.80	0.80	0.90
5	0.152	0.166			0.50	0.50	0.50	0.70	0.90	0.90	
6	0.191	0.191			0.80	0.50	0.80	0.80			
7	0.50	0.50				0.80	0.90	0.90			
8	0.50	0.50									
9	0.50	0.50									
10-15	0.50	0.50									

[a] Mortality rates for ages 0-6 taken from a model of lake trout in Wisconsin's Lake Superior management zone WI-2 (Ebener et al. 1990); mortality rates for ages 7-15 were means from recent estimates based on large mesh gill netting in MN waters of Lake Superior (Schreiner et al. 1988, 1989, 1990).

[b] Mortality over 160 days; from day of fingerling stocking on 29 October to 31 May.

[c] Mortality over 107 days; from fry stocking on 1 June to 15 September (Close, in review). On about 15 September, 0.39% of the number stocked became age 0 emigrants (see text).

[d] Mortality over first 259 days in lake, from 15 September to 31 May.

[e] Mortality from parr to age 2 and age 3 emigrants (Hassinger et al. 1974). Fish remaining from each year class became age 2 emigrants (80%) or age 3 emigrants (20%) (Hassinger et al. 1974).

[f] Mortality for fry over 2 years of stream life.

[g] Mortality for spring yearlings (plus age 2 emigrants from fry stocking), over 122 days from 1 June yearling stocking to 30 September.

[h] Mortality for spring and fall yearlings (plus age 2 emigrants) over 243 days from 1 October yearling stocking to 31 May.

[i] Mortality over 2 years of stream life (see text).

APPENDIX E: Sensitivity Analysis.

Table E1.--Sensitivities of estimated cumulative consumption by individual fish to deviation of input variables. Simulations were done on one age 7 lake trout, one each age 1/2, age 2/3, and age 3/3 steelhead, one age 5 Kamloops, one each of fry-stocked, fingerling-stocked, and yearling-stocked Atlantic salmon in their third lake year, one age 3 chinook salmon, and one age 1 coho salmon in Minnesota waters of Lake Superior, all with an all-smelt diet. A range of values is given for species which were tested in more than one life history variation.

Variable	Input modification	
	+10%	-10%
	Lake trout	
Prey caloric density	- 9.46%	+11.81%
Indigestible fraction	+ 0.36%	- 0.36%
Temperatures (all)	+ 4.24%	- 3.19%
Weights (start and final)	+ 8.73%	- 6.83%
Final weight	+19.66%	-19.06%
Proportion of weight lost during spawning	+ 1.17%	- 1.16%
Spawning		-11.06%[a]
	Steelhead	
Prey caloric density	- 9.50 to - 9.57%	+11.72 to +11.80%
Indigestible fraction	+ 0.36 to + 0.41%	- 0.36 to - 0.42%
Temperatures (all)	+ 5.35 to + 6.60%	- 4.48 to - 5.30%
Weights (start and final)	+10.27 to +10.62%	-10.13 to -10.42%
Final weight	+11.90 to +13.73%	-11.61 to -13.30%
Proportion of weight lost during spawning	+ 0.84 to + 1.04%	- 0.83 to - 1.02%
Spawning		- 7.77 to - 8.97%[a]
	Kamloops	
Prey caloric density	- 9.49%	+11.81%
Indigestible fraction	+ 0.30%	- 0.30%
Temperatures (all)	+ 6.28%	- 5.62%
Weights (start and final)	+10.51%	-10.29%
Final weight	+15.84%	-15.04%
Proportion of weight lost during spawning	+ 1.09%	- 1.07%
Spawning		- 9.93%[a]
	Atlantic salmon	
Prey caloric density	- 9.54 to - 9.59%	+11.69 to +11.76%
Indigestible fraction	+ 0.36 to + 0.37%	- 0.36 to - 0.37%
Temperatures (all)	+ 4.67 to + 4.76%	- 4.32 to - 4.41%
Weights (start and final)	+ 9.79 to +10.20%	- 9.70 to -10.17%
Final weight	+12.60 to +14.05%	-12.33 to -13.68%
Proportion of weight lost during spawning	+ 0.20 to + 0.23%	- 0.20 to - 0.23%
Spawning		- 1.97 to - 2.26%[a]

Table E1.--Continued.

Variable	Input modification +10%	 -10%
Chinook salmon		
Prey caloric density	-10.11%	+12.95%
Indigestible fraction	+ 0.39%	- 0.39%
Temperatures (all)	+ 2.46%	- 1.85%
Weights (start and final)	+12.20%	-11.69%
Final weight	+13.82%	-13.03%
Coho salmon		
Prey caloric density	- 9.84%	+12.39%
Indigestible fraction	+ 0.38%	- 0.37%
Temperatures (all)	+ 2.06%	- 1.96%
Weights (start and final)	+10.28%	-10.17%
Final weight	+10.05%	- 9.91%

[a] Spawning eliminated (i.e. weight loss due to spawning = 0).

APPENDIX F: Simulation Model Outputs.

Table F1.--Total cumulative consumption (g) of 5 diet categories by all year classes of salmonines during modeling year 1989. Modeling group distinguishes sub-categories within species which were modeled separately due to size or life history differences. MT = metric tonne = 1,000,000 g.

		Diet Item				
Species	Modeling Group	Smelt	Coregonines	Insects	Crustaceans	Other fish
Lake trout	Native	1.705×10^{8}	1.918×10^{7}	2.977×10^{7}	4.236×10^{7}	1.419×10^{7}
	Stocked	1.423×10^{9}	1.877×10^{8}	1.188×10^{8}	1.174×10^{8}	1.224×10^{8}
Chinook salmon		7.266×10^{8}	1.617×10^{7}	5.478×10^{7}	9.195×10^{7}	3.555×10^{7}
Coho salmon		2.309×10^{8}	2.263×10^{7}	5.925×10^{7}	3.063×10^{7}	5.763×10^{7}
Steelhead	Age 0 emigrants	2.555×10^{6}	0	6.948×10^{6}	0	0
	Age 2 emigrants	2.114×10^{7}	0	5.535×10^{7}	0	0
	Age 3 emigrants	6.436×10^{6}	0	1.698×10^{7}	0	0
Kamloops		1.465×10^{8}	0	3.629×10^{8}	0	0
Atlantic salmon	Stocked as fry	4.463×10^{6}	1.767×10^{5}	7.629×10^{4}	3.433×10^{5}	0
	Stocked as fingerlings	2.280×10^{7}	9.389×10^{5}	3.421×10^{5}	1.539×10^{6}	0
	Stocked as yearlings	5.870×10^{7}	2.333×10^{6}	9.912×10^{5}	4.460×10^{6}	0
Total Consumption (g)		2.814×10^{9}	2.491×10^{8}	7.062×10^{8}	2.887×10^{8}	2.298×10^{8}
Total Consumption (MT)		2814.0	249.1	706.2	288.7	229.8

Table F2.--Lifetime consumption (g) per 100,000 fish stocked.

Species	Stocking Size	Diet Item				Other fish
		Smelt	Coregonines	Insects	Crustaceans	
Lake trout	fall Fgl	$5.076x10^7$	$6.473x10^6$	$5.431x10^6$	$4.955x10^6$	$4.397x10^6$
	spring Yrl	$4.880x10^8$	$6.346x10^7$	$4.272x10^7$	$3.726x10^7$	$4.285x10^7$
Chinook salmon	Fry or Fgl	$1.473x10^8$	$3.275x10^7$	$1.115x10^7$	$1.853x10^7$	$7.172x10^6$
Steelhead	Fry	$1.329x10^6$	0	$3.504x10^6$	0	0
Kamloops	Fry	$7.071x10^6$	0	$1.859x10^7$		
	spring Yrl	$7.071x10^7$	0	$1.859x10^8$	0	0
	fall Yrl	$1.154x10^8$	0	$2.639x10^8$	0	0
Atlantic salmon	Fry	$1.423x10^7$	$5.617x10^5$	$2.454x10^5$	$1.104x10^6$	0
	Fgl	$3.406x10^7$	$1.360x10^6$	$5.666x10^5$	$2.550x10^6$	0
	Yrl	$1.549x10^8$	$6.216x10^6$	$2.537x10^6$	$1.142x10^7$	0

Table F3.--Age of greatest impact on forage base of Lake Superior.
Fgl = Fingerling, Yrl = Yearling.

Species	Stocking Size	Age at which greatest total consumption occurs
Lake trout	Fgl	6
	Yrl	6
	(native)	6
Chinook salmon	Fry or Fgl	2
Coho salmon	(naturalized)	1
Steelhead	Fry	3[a]
Kamloops	Fry	3[a]
	Yrl	1
	fall Yrl	1
Atlantic salmon	Fry	2
	Fgl	1
	Yrl	1

[a] Total age reported; reflects impact of all stocked fry regardless of time spent in stream.

Table F4.--Cumulative consumption (g) of rainbow smelt and coregonines by one individual of each species and stocking size. Consumption by steelhead was reported for individuals that emigrate to the lake at age 2. Native lake trout and stocked Yrl consumed at rates similar to stocked Fgl. Kamloops fall Yrl and spring Yrl consumed at similar rates. (Fgl = Fingerling, Yrl = Yearling)

On 31 May	Lake trout	Chinook salmon	Coho salmon	Steelhead	Kamloops	Atlantic salmon		
at age:	Fgl	Fry or Fgl	Naturalized	Fry	spring Yrl	Fry	Fgl	Yrl
1	19.2	448.2						213.7
2	129.8	2,862.4			898.7		2,923.7	2,705.2
3	613.1	10,472.2	1,914.1	851.8	3,398.2	2,689.8	8,170.1	6,241.2
4	1,397.2	25,663.8	3,519.5[b]	3,019.5	6,731.4	6,225.8	13,782.6	11,487.6
5	2,878.9	33,731.2[a]		6,294.5	10,665.4	11,472.2		17,076.4
6	5,082.8			9,904.4	13,895.3	17,061.0		
7	7,830.8			13,441.1	17,619.5			
8	10,703.9			16,863.5	21,655.4			
9	13,935.6							
10	17,190.6							
11	20,995.1							
12	26,187.7							
13	31,733.2							
14	36,722.6							
15	41,926.3							
16	47,344.4							

[a] Consumption total at spawning time, 30 October, at age 4.
[b] Consumption total at spawning time, 1 November, at age 3.

APPENDIX G: Forage Base.

Table G1.--Forage fish populations in Minnesota waters of Lake Superior, sampled by the National Fisheries Research Center, Ashland Biological Station, Wisconsin. Total spring biomass accounts for the fish within the 15-70 m depth contours, and corrected total biomass accounts for all depths. Production was calculated using estimated P/B ratios. B for 1990-1991 was assumed equal to B in 1990. MT = metric tonne = 1,000,000 g.

Year	Mean weight per individual (g)	g/hectare	Total spring biomass (MT)	B Corrected total biomass (MT)	P Production (MT)	B+P Total biomass available for consumption in one year (MT)
			Rainbow smelt			
1985	1.5	1,436.9	37.70	54.17	38.60	92.77
1986	5.9	425.0	11.15	16.02	150.44	166.46
1987	5.9	6,831.8	179.23	257.51	196.32	453.83
1988	4.7	2,637.6	69.20	99.43	64.94	164.37
1989	1.5	494.8	12.98	18.65	58.80	77.45
1990	2.4	2,341.6	61.43	88.26	97.09	185.35
			Lake herring			
1985	7.5	8.3	0.22	0.32	1.31	1.63
1986	18.1	90.6	2.38	3.43	2.00	5.43
1987	7.5	60.1	1.58	2.28	0.80	3.08
1988	0	0	0	0	17.64	17.64
1989	9.1	1,333.2	34.98	50.40	30.37	80.77
1990	4.2	962.1	25.24	36.37	25.46	61.83
			Bloater			
1985	2.7	6.5	0.17	0.37	0.13	0.50
1986	0	0	0	0	0.44	0.44
1987	4.2	22.3	0.59	1.27	0.45	1.72
1988	3.0	0.3	0.01	0.02	1.05	1.07
1989	6.7	52.7	1.38	2.97	1.04	4.01
1990	0	0	0	0	0	0

APPENDIX H: Ration and Growth Evaluation.

Table H1.--Baseline P values (proportion of maximum ration consumed) based on current temperature and body size.

Age	Lake Trout	Chinook Salmon
0	0.751956	0.476638
1	0.516988	0.584602
2	0.573997	0.752307
3	0.373945	0.848866
4	0.490182	0.467493
5	0.508979	
6	0.493273	
7	0.413329	
8	0.449554	
9	0.414577	
10	0.448717	
11	0.543656	
12	0.512652	
13	0.430279	
14	0.432783	
15	0.435353	

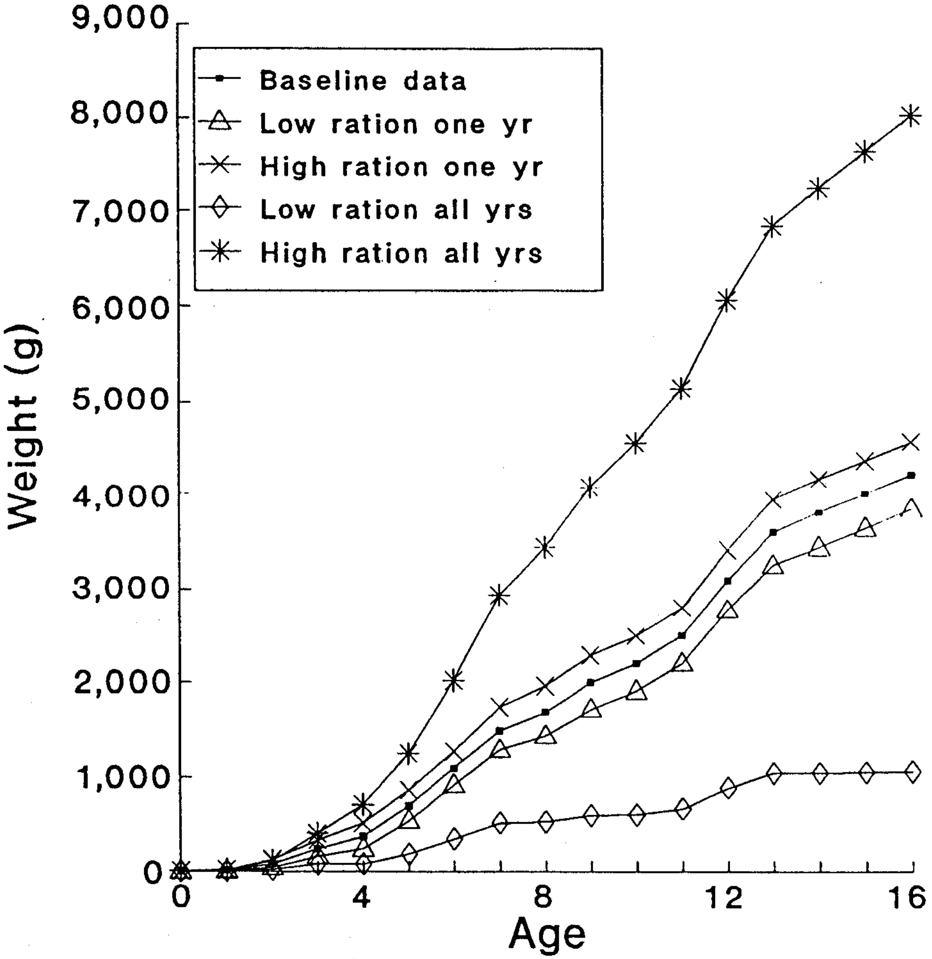

Figure H1.--Lake trout growth at various ration levels. Baseline P values (Table H1) were increased or decreased by 0.1 to simulate the growth of each year-class under conditions of increased or decreased prey availability. Simulations beginning with baseline starting weights were run for each year-class for a period of one year at increased and decreased ration. Simulations were also run for the entire lifespan at increased or decreased rations, using final weights from each year as starting weights for the next year.

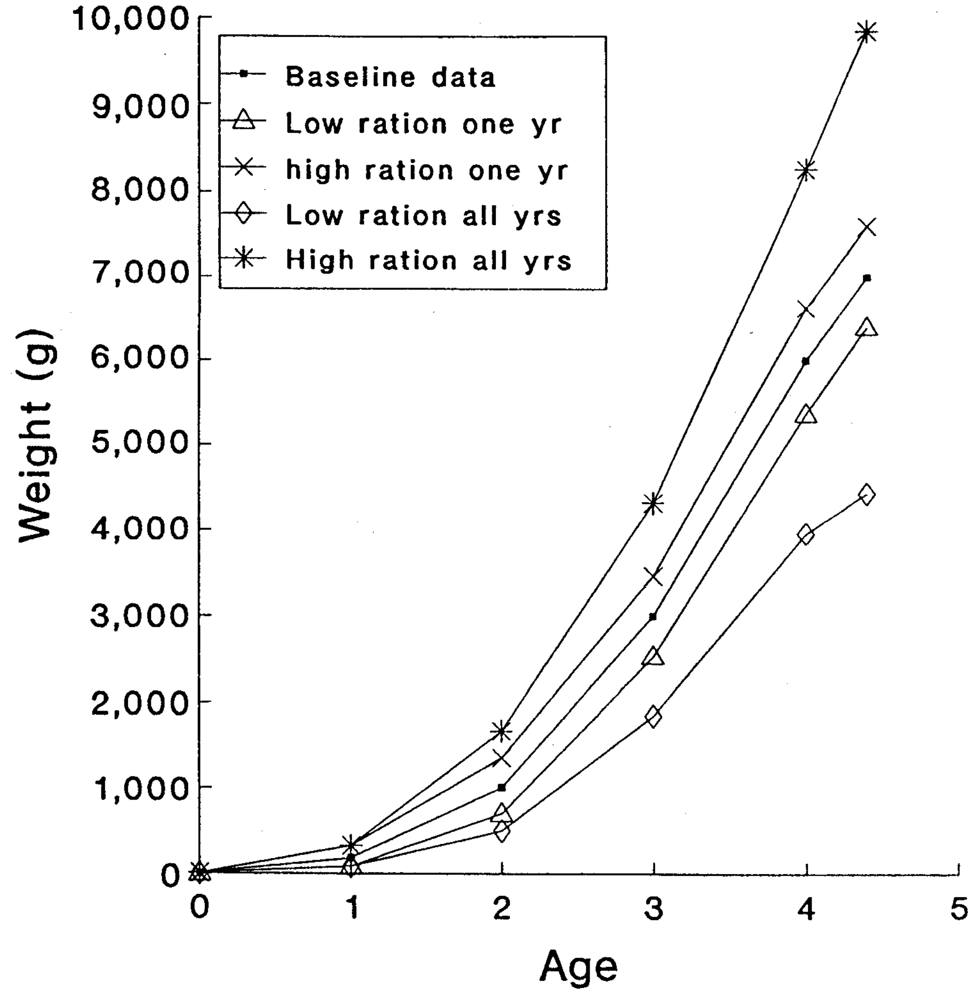

Figure H2.--Chinook salmon at various ration levels. Baseline P values (Table H1) were increased or decreased by 0.1 to simulate the growth of each year-class under conditions of increased or decreased prey availability. Simulations beginning with baseline starting weights were run for each year-class for a period of one year at increased and decreased ration. Simulations were also run for the entire lifespan at increased or decreased rations, using final weights from each year as starting weights for the next year.

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