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Chinook Salmon (*Oncorhynchus tshawytscha*) Population
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Darren Matthew Benjamin

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James R. Bence
Major professor

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CHINOOK SALMON (*Oncorhynchus tshawytscha*) POPULATION DYNAMICS IN LAKE MICHIGAN, 1985 TO 1996

By

Darren Matthew Benjamin

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ABSTRACT

CHINOOK SALMON (*Oncorhynchus tshawytscha*) POPULATION DYNAMICS IN LAKE MICHIGAN, 1985 TO 1996

By

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Chinook salmon remains a popular sport fish in Lake Michigan despite the collapse of the chinook fishery beginning in 1987. This collapse is widely believed to have been caused by a combination of nutritional stress and mortality from bacterial kidney disease (BKD). This study involved a spatial analysis of trends in the chinook fishery, and a lake-wide stock assessment model for chinook salmon. Fishery trend analysis shows that declines in the fishery were more severe in the western regions of the lake than in the eastern regions. Evidence suggests that these spatial differences in fishery trends were due to changes in chinook spatial distribution rather than differences in mortality.

I built a stock assessment model for chinook salmon in Lake Michigan using 1985-1996 recreational fishery data in order to estimate population abundance, fishing mortality, and time-varying natural mortality. This statistical catch-at-age analysis model is fit to observed recreational fishery and weir return data. Results indicate that the natural mortality rate increased from 1986 to 1993, and declined from 1994 to 1996. These results are inconsistent with estimates of BKD incidence from harvest weirs, suggesting that causes of changing natural mortality are not entirely due to BKD, and may be more complex than previously considered.

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CHAPTER ONE

INTRODUCTION

The chinook salmon (*Oncorhynchus tshawytscha*) has been an important top predator in the Lake Michigan fish community for 30 years. In addition, their size and fighting ability have made them a prized sport fish, and their presence in the lake has helped to support a multi-million dollar fishing industry. In the late 1980's the future of chinook salmon in the lake was in question when thousands of fish died from bacterial kidney disease (BKD), and lakewide harvest declined.

Today, increases in chinook salmon salmon harvest may be an indication that the population is beginning to show signs of recovery. Nevertheless, fundamental questions remain regarding the future of fishery management in Lake Michigan. Among these questions is: "How can similar problems be avoided in the future?" This thesis addresses the Lake Michigan chinook salmon fishery from 1985 to 1996 in order to understand the response of the fishery to changes in the fish population. An analysis of chinook salmon population dynamics using a stock assessment model provides an additional understanding of trends in mortality and abundance.

The Lake Michigan fish community has changed dramatically in the past 60 years, and continues to change today (Eshenroder et al. 1995). Prior to the 1950's, the fish community consisted mostly of species endemic to the Great Lakes or its tributaries.

The inshore fish communities of Green Bay and other shallow embayments and large river estuaries included lake sturgeon (*Acipenser fulvescens*), emerald shiner (*Notropis atherinoides*), suckers (*Catostomus* sp.), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum vitreum*). The pelagic fish community included planktivorous lake herring (*Coregonus artedi*) and six species of deepwater ciscoes (*Coregonus* sp.), two of which had already suffered population declines prior to 1900 (Smith 1968). Lake trout (*Salvelinus namaycush*) was the dominant piscivore of the pelagic community, and was the major piscivore along with the burbot (*Lota lota*) in the benthic community. Lake trout and burbot preyed upon adult deepwater ciscoes and deepwater sculpin (*Myoxocephalus thompsoni*) in the benthic community.

Commercial fishing, habitat destruction, and invasions by exotic species disrupted the fish community in the 1940's and 1950's (Smith 1972). Parasitism by the exotic sea lamprey (*Petromyzon marinus*) contributed largely to the decline of lake trout and burbot. The decline of these piscivores allowed the exotic alewife (*Alosa pseudoharengus*) to flourish. The presence of alewife continued to disrupt the fish community, as alewife preyed upon the larval fish of native species including: deepwater ciscoes, emerald shiner, lake herring, yellow perch, deepwater sculpin, spoonhead sculpin (*Cottus ricei*), burbot, and lake trout (Eck and Wells 1987; Crowder 1980; Eshenroder et al. 1995; Krueger et al. 1995; Mason and Brandt 1996). By the 1960's, the fish biomass in the lake was dominated by alewife and another exotic species, rainbow smelt (*Osmerus mordax*).

The Great Lakes Fishery Commission began a sea lamprey control program in 1960, and by the late 1960's successfully reduced the sea lamprey population in Lake Michigan to 10-20% of its pre-1960 level (Holey et al. 1995). With sea lamprey numbers reduced, and an overabundance of alewives, stocking programs for lake trout and Pacific salmon were initiated beginning in 1963. Five major salmonines have been stocked: lake trout, chinook salmon, coho salmon, rainbow trout (steelhead), and brown trout. Brook trout and splake (brook x lake hybrids) have been stocked in smaller quantities. Lake trout were stocked with the goal of reestablishing self-sustaining populations. The other salmonines were introduced as a biological control for alewives, and to provide a recreational fishery (Tody and Tanner 1966). The combination of predation by salmonines and low recruitment effectively reduced the alewife population by the early 1980's (Eck and Wells 1987; Jude and Tesar 1985). Increases in abundance of native species including bloater, yellow perch, and deepwater sculpin, followed the decline of alewives (Eshenroder et al. 1995).

Chinook Salmon Biology

Chinook salmon were first successfully stocked in the Michigan waters of Lake Michigan in 1967. Broodstock originated from Oregon and Washington, and after three years of stocking, Michigan became self-sufficient in the collection of eggs from Lake Michigan chinook salmon. Michigan supplied eggs to Wisconsin from 1969 to 1971, and to Illinois and Indiana beginning in 1970 (Keller et al. 1990). Illinois and Indiana continue to stock chinook salmon from eggs collected at Michigan weirs.

Chinook salmon eggs are collected from mature fish returning to harvest weirs from September through November. Fry are raised in hatcheries, and are stocked in the following April and May as fingerlings, just prior to reaching their critical smolt life stage. Chinook salmon smolts undergo physiological changes that prepare them for life in a large lake or ocean environment, and it is during the smolting process that chinook salmon imprint on their natal streams.

Chinook salmon are semelparous, and generally complete their life cycle by returning to the streams from which they were born (or stocked). Young-of-the-year chinook salmon reside in the stream over the winter and early spring months. Natural reproduction was observed as early as 1973, and is now significant enough to warrant management consideration (Rybicki 1973; Taube 1974; Elliott 1994). Improvements in stream habitat, such as dam removal, run-of-the-river flow regulation, and bank stabilization, probably contributed significantly to increases in natural reproduction in the 1980's. Today the annual wild smolt production is estimated at 2.2 million fish (Rutherford 1997), and the contribution of wild chinook salmon to the sport fishery is estimated to be 30% (Hesse 1994).

Natural reproduction is primarily limited to streams tributary to the Michigan waters of Lake Michigan. Most of Wisconsin's tributaries to Lake Michigan are blocked by dams, lack suitable spawning substrate, and have large water level fluctuations (Avery 1974). Illinois and Indiana streams also lack suitable spawning substrate.

Chinook salmon are relatively short-lived in Lake Michigan. Nearly all fish mature by age-5, while some precocious males (jacks) mature at age-1. In the late 1980s, age-3 fish dominated the sport harvest and the weir harvest. Today, harvest is dominated by 2-year olds. Chinook salmon growth rates may be density-dependent. Mean weight and mean length increased for older fish after the collapse of the fishery, suggesting that a reduction in the population alleviated competition for food (Wesley 1996).

Within-lake estimates of mortality rates are not well documented for chinook in Lake Michigan (Keller et al. 1990). Chinook salmon are faced with natural mortality from different sources at different life stages. Probably the most critical life stage is from age-0 to age-1, during which time chinook salmon are either stocked or spawned and must make the journey to the lake. Survival of these young-of-the-year fish varies spatially and temporally. Carl (1984) estimated a daily instantaneous mortality rate of 0.025 for wild juveniles in two Michigan tributary streams. Seelbach (1985) estimated a planting to smolting mortality of 0-32% for hatchery chinook salmon in the Little Manistee River. Variability in survival of young-of-the-year chinook salmon in Lake Michigan is influenced by predation, water temperature, and date, location, and density of stocked fingerlings (Clark 1996).

Mortality from diseases and parasitism has been implicated as the major cause of the decline in the chinook salmon population in the late 1980's. Dead adult chinook salmon began to wash up on the Lake Michigan shoreline beginning in the spring of 1986. Reports of dead fish on the beaches began in the southern end of the lake in the spring and moved progressively northward during the season, as fish were carried by strong South-to-North currents. The majority of sick fish examined had severe clinical signs of bacterial kidney disease (BKD), which was considered the final cause of death. Because BKD occurs naturally in chinook salmon populations and does not necessarily cause mortality, it is believed that some unknown stress weakened the fish and caused BKD to become lethal. Many believe that this unknown stress was due to the decline in alewife abundance, which may have caused nutritional stress and increased susceptibility to disease (Marcquenski et al. 1997; Rybicki and Clapp 1996; Stewart and Ibarra 1991).

The number of visible deaths was estimated to be at least 10,000 fish in 1988, and at least 20,000 fish in 1989 (Nelson and Hnath 1990; Johnson and Hnath 1991). Nelson and Hnath (1990) noted that the number of BKD-related deaths was small relative to the fishery harvest, and suggested that these deaths would not affect the fishery. However, an estimate does not exist of the number of BKD-related deaths that remained in the bottom of the lake instead of washing up on the shore. The total number of BKD-related deaths, including those that do not wash ashore, is likely to be much higher than previously reported (Nelson and Hnath 1990).

Fishing mortality is not considered to be the major source of mortality in Lake Michigan chinook salmon (Rutherford 1997). The sport fishery grew rapidly through the 1970's and early 1980's, as the number of stocked salmonines increased and as fishing technology developed and anglers improved at targeting salmonines (Hansen et al. 1990). Fishing effort for salmonines peaked in the mid-1980's before declining by 63% from 1986 to 1992. Salmonine effort has been relatively stable from 1992 to 1996. A more detailed analysis of trends in the sport fishery is presented in Chapter 2.

Mortality from commercial fishery harvest of chinook salmon is low in comparison to sport fishery harvest. Commercial harvest is limited to tribal fishery harvest in the northern region of the lake and Grand Traverse Bay (Schorfhaar 1997; Keller et al. 1990). From 1983 to 1987, annual tribal harvest of chinook salmon in the Northern region of the lake ranged from 300 to 900 fish, or 4,000 to 10,000 pounds (Keller et al. 1990). In contrast, estimated sport harvest of chinook salmon exceeded 8 million pounds annually over the same period (Francis 1996).

Mature chinook salmon that return to tributary streams are either harvested at the weirs, harvested by the stream fishery, or die naturally from spawning-related mortality. Chinook salmon that return to streams with harvest weirs can be counted in order to obtain an index of abundance of spawning fish. Data from Wisconsin weirs show a peak in chinook salmon returns in 1987, followed by a sharp decline in 1989 (Eggold et al. 1997). This decline in chinook salmon returns from 1987 to 1989 corresponds with the increase in natural mortality observed in the spring of 1988 and 1989, suggesting that chinook salmon died before maturing and returning to the weirs.

Within-lake movements of chinook salmon have not been quantified. Patterns in survey harvest rates suggest a seasonal northward movement from spring to summer along the eastern shore (Jonas and Clapp 1998). Harvest rates also suggest an east to west movement in the summer and back again in the fall (Elliott 1993). Winter temperatures and forage abundance and distribution can influence these movement patterns (Elliott 1993; Keller et al. 1990). Coded wire tagged (CWT) chinook salmon recovered from the sport fishery indicated movements both within-lake and between-lakes. Chinook salmon planted in Michigan's waters of Lake Michigan appeared in the sport harvest in Wisconsin, Illinois, Indiana, and Michigan, as well as in Lake Huron. However, CWT chinook salmon planted in Wisconsin's waters were widely dispersed in western Lake Michigan, but were not readily available to anglers in eastern Lake Michigan (Lychwick 1985; Keller et al. 1990).

Goals and Objectives

The goal of this project is to understand the population dynamics of chinook salmon in Lake Michigan and how these dynamics affect the sport fishery. It is intended that this will serve as groundwork toward future modeling efforts that incorporate other salmonine predators and their trophic interactions with forage fishes in Lake Michigan (e.g. Rutherford 1997; Koonce and Jones 1991). Additionally, information on recruitment, harvest, and mortality, as derived from the stock assessment model, should help improve the management of chinook salmon in Lake Michigan.

The objectives of this project were: (1) develop a lake-wide database of stocking and harvest information for all salmonines in Lake Michigan, with the intention that other salmonine species will be similarly analyzed in the future; (2) analyze trends in the chinook salmon sport fishery and make inferences about spatial patterns of abundance and mortality; (3) build an age-structured stock assessment model specific to Lake Michigan chinook salmon, drawing from existing catch-at-age models (e.g., Fournier and Archibald 1982; Methot 1990); (4) evaluate temporal variations in recruitment and mortality of chinook by fitting the model to available data; (5) understand the limits of parameter estimates as they are applied to the model; (6) evaluate the potential importance of incorporating lakewide spatial variation of mortality into the model.

The following chapters are divided into three sections. Chapter 2 is an analysis of trends in the salmonine sport fishery, with a particular emphasis on chinook salmon. Chapter 3 is a lake-wide stock assessment model I built for chinook salmon in order to quantify mortality rates and abundance. The final chapter is a discussion of a spatial stock assessment model, implications for management, and directions for future research.

CHAPTER TWO

SPATIAL AND TEMPORAL CHANGES IN THE LAKE MICHIGAN CHINOOK SALMON FISHERY, 1985-1996.

Introduction

The present Lake Michigan fish community is complex and dynamic. The 1940s and 1950s were periods of dramatic change, as native lake trout (*Salvelinus namaycush*) and cisco (*Coregonus sp.*) populations either declined or became extinct due to invasions by exotic species, commercial overfishing, and degraded spawning habitat (Wells and McLain 1973). By the late 1950s, the fish community was of little economic or recreational value. Successful management efforts to control exotic sea lamprey (*Petromyzon marinus*), as well as the need to control overabundant alewives (*Alosa pseudoharengus*), opened the door for the introduction of trout and Pacific salmon in the 1960s. The introduction of salmonines served several purposes: to restore lake trout, to control nuisance alewives, and to support a sport fishery (Tody and Tanner 1966).

Lake Michigan's modern salmonine stocking program began with the successful introductions of rainbow trout (steelhead) (*Oncorhynchus mykiss*) in 1963. Lake trout were re-introduced in 1965. Coho salmon (*O. kisutch*), brown trout (*Salmo trutta*), and brook trout (*S. fontinalis*) were introduced in 1966, followed by chinook salmon (*O. tshawytscha*) in 1967. Stocking of all salmonines increased from the 1960s to the 1980s.

Stocking rates by some states increased more slowly or even declined in the mid-1980s due to limits in hatchery production capacity and increased concerns about lake carrying capacity (Keller et al. 1990; Kitchell and Crowder 1986; Stewart et al. 1981). Lake-wide stocking of all salmonines has been relatively constant since the late 1980's (Keller et al. 1990; Holey 1996).

The salmonine sport fishery grew rapidly through the 1970s and 1980s; angler effort increased by an order of magnitude, harvest rate doubled, and harvest increased 20-fold in the Wisconsin waters of Lake Michigan (Hansen et al. 1990). Much of the fishery growth was driven by increases in annual stocking of salmonines. Of these salmonines, chinook salmon was the most heavily stocked and was the most prized sportfish because of its size and fighting ability. By the mid-1980s, Lake Michigan supported the most spectacular sport fishery in its history and contributed to an estimated $2 billion Great Lakes fishery (Keller et al. 1990).

As stocking levels continued to grow through the 1970s, biologists became concerned that high levels of stocking would produce a predator-prey system in which predator abundance would not be governed by prey dynamics, and leading to instability (Stewart et al. 1981). Stewart et al. (1981) challenged Lake Michigan fishery managers to consider temporal fluctuations in forage biomass and species composition when determining stocking levels. Michigan created a plan to reduce forage consumption by 10% by reducing its overall stocking by 8.5% relative to the 1980-84 average, beginning in 1985 and extending through 1990 (Keller et al. 1990). Wisconsin in turn planned to reduce chinook salmon stocking rates by 10% in response to declines in the species' condition and in alewife abundance (Hansen 1986; Keller et al. 1990).

In 1986 and 1987, dead chinook salmon were littering beaches along the southeastern shoreline. By 1988, the number of visible dead chinook salmon was estimated at 10,000 fish (Nelson and Hnath 1990; Johnson and Hnath 1991), and increased to an estimated minimum of 20,000 in 1989. Clinical tests indicated that these fish ultimately died from an infestation of *Renibacterium salmoninarum*, a bacterium that causes bacterial kidney disease (BKD) (Nelson and Hnath 1990). Because *R. salmoninarum* is common even in healthy salmon, it is believed that some other environmental stress weakened these fish to the point where BKD became lethal (Nelson and Hnath 1990). It has been suggested that the additional stress is nutritional stress from a reduced alewife population (Jones et al. 1993; Nelson and Hnath 1990; Rybicki and Clapp 1996; Stewart and Ibarra 1991; Wesley 1996). Chinook salmon continue to die from BKD today (Clark 1996), although the presence of dead chinook on the beaches has declined (Marcquenski 1997). Increases in natural mortality of chinook salmon were reflected in the sport fishery, as harvest rates, harvest, and fishery effort declined beginning in 1987. By 1993, Lake Michigan chinook salmon harvest had severly declined despite the maintenance of high stocking levels.

The purpose of this study is to describe more fully the spatial and temporal trends in the Lake Michigan chinook salmon fishery from 1986 to 1996, within the context of the entire salmonine fishery. A better understanding of the extent and location of harvest declines, as well as a spatial understanding of fishing mortality and chinook salmon movements will aid in stocking decisions and in population modeling.

Methods

Stocking Data

Information on salmonine stocking was provided by Lake Michigan fishery management agencies. Illinois stocking data was provided by Rich Hess (Illinois Department of Natural Resources). Indiana stocking data was compiled from Indiana DNR stocking reports provided by Jim Francis (Indiana Department of Natural Resources). Michigan stocking information from 1963 to 1978 was compiled from summarized data provided by Bill McClay (Michigan Department of Natural Resources). Stocking information from 1979 to 1996 was provided by Christine Larson through the Fish Stocking Information System (Michigan Department of Natural Resources). Wisconsin stocking information was compiled from Wisconsin DNR summary reports (Hansen et al. 1991; Coshun 1991; Hansen 1988; Burzynski and Multhauf 1995; Burzynski 1996).

Compiled lake-wide data was entered into a database and error-checked for accuracy. The database was compared to an existing Lake Michigan stocking database developed for the Great Lakes Fishery Commission (M. Holey, USFWS, personal communication). The existing GLFC database was missing data for rainbow trout from 1963 to 1974, for brook trout from 1966 to 1975, and for brown trout from 1966 to 1974. The GLFC database covered stocking of chinook salmon from 1967, and coho salmon from 1966. For stocking years included in both databases, differences in stocking numbers across databases were generally minor. For example, chinook salmon stocking data differed in only 5 years between 1967 and 1988, and differences in those years were less than 7%. Coho salmon stocking differed in 9 of the years between 1966 and 1988, and most of those differences were less than 7% except for 1966 (60%) and 1985 (20%). Discrepancies were most commonly due to double entry errors in the GLFC database, while in other minor cases the GLFC database contained records of additional plants that I could not account for. This second situation is not surprising since most of my stocking numbers originated from summary reports and not raw data. Still, any errors in my database would have originated within the summary reports themselves. The GLFC database contained stocking records up through 1988 for all species except lake trout, which contained records through 1992. My database contains records from 1963 to 1996 for all salmonines except lake trout. Results of this comparison and copies of the updated database were presented to the Lake Michigan Technical Committee in 1996.

Monitoring of the Sport Fishery

Data and estimates on sport fishery harvest, effort, and catch rates were carefully reviewed. There are two primary sources for these data. The first is from creel surveys run by each of the states and the second source is from mandatory reports obtained from charter operators. I begin by discussing data and estimates for the creel surveys run by each of the state resource agencies. In Michigan, Illinois, and Wisconsin, these creel surveys explicitly exclude the charter component (before 1990, Michigan's charter fishery was covered as part of the creel survey). The charter trips are included as part of the Indiana creel survey and these data are used to evaluate that component of the fishery. For the other states, information on the charter component of the fishery comes from mandatory charter reports.

Creel survey data and estimates

Annual creel surveys are conducted by each of the states surrounding Lake Michigan in order to monitor the sport fishery. Consistent estimates of total effort and harvest are available from 1986 to the present. Wisconsin conducted a creel survey of the salmonid fishery in the Wisconsin waters of Lake Michigan from 1969 to 1985 (Hansen et al. 1990), and began sampling the entire fishery in 1986. Illinois began consistently sampling its fishery in 1986, though additional surveys were done in 1985, 1979, and 1969. Indiana has sampled its portion of Lake Michigan annually beginning in 1974, though sampling methods have been consistent since 1986. Michigan began consistently monitoring its Lake Michigan fishery in 1985.

Austen et al. (1995) compare and contrast the creel survey methods from each of the states. Creel surveys on Lake Michigan are generally conducted from April through October, and ice fisheries on Green Bay and Grand Traverse Bay are occasionally sampled as well. Each survey approximates a two-stage sampling design, with sampled days treated as the first stage, and counts or interviews within days treated as the second stage. Sampling is stratified by period (month or similar interval), day type (weekday or weekend/holiday), area (port, site, or management area), and fishing mode (boat, pier, shore, stream, etc.). I grouped the boat fishery to include data estimates from surveys of launched boats, moored boats, and charter boats (see *Charter report data*). The shore fishery included surveys of shore, pier, and ice fishery anglers. The stream fishery was not included in this study due to a lack of information for Michigan's stream fishery.

Fishing effort is estimated from interval counts at access sites or from instantaneous counts of boats, pedestrian anglers, ice shanties, cars, or trailers. Average daily counts are converted to a measure of fishing effort (angler-hours), and fishing effort is estimated for a stratum by multiplying the average daily effort by the number of days in the stratum. Harvest rates (harvest per angler-hour) are calculated from the angler interviews within each stratum, and are multiplied by fishing effort to estimate harvest for a stratum. Summary harvest rates reported here are calculated by dividing the sum of the annual harvest by the sum of the annual effort. Variances are available for Michigan and Wisconsin's surveys only. For Wisconsin, variances were provided by the WDNR for total harvest by species and total fishery effort. For Michigan, variances were calculated for total harvest and targeted harvest by species, total effort, and salmonine effort. Standard errors are reported here for Michigan and Wisconsin regions only.

Changes in harvest rates, or catch-per-unit-effort (CPUE), can be used to assess trends in relative abundance. In spite of drawbacks in using CPUE as an index of abundance (Malvestuto 1983), this is necessary in Lake Michigan since there is no lake-wide fishery-independent survey for salmonines. In Lake Michigan, the sport fishery effort is primarily directed towards salmonines and yellow perch. Targeted harvest rates are used in this study to avoid bias due to changes in contribution of effort for yellow perch or other species. Targeted effort is defined as effort directed at the harvest of salmonines. Targeted harvest is estimated from targeted effort, and targeted harvest rates are calculated as the quotient of targeted harvest and targeted effort.

Summary information on the sport fishery was provided by biologists from Wisconsin, Illinois, and Indiana. Wisconsin data was provided by Brad Eggold (Wisconsin Department of Natural Resources). Illinois creel data was obtained from annual summary reports (e.g. Brofka and Marsden 1997), and additional data was provided by Wayne Brofka (Illinois Natural History Survey). Illinois charter fishery data was provided by Rich Hess (Illinois Department of Natural Resources). Indiana data was obtained from annual summary reports (Braun 1987; Palla 1997), and for recent years was provided by Jim Francis (Indiana Department of Natural Resources).

Michigan's creel survey estimates were recalculated from the raw data for this study. Pre-existing methods utilized a mean-of-ratios catch rate estimator that is inappropriate for Michigan access point angler surveys (Lockwood 1997). I recalculated estimates for Michigan's waters of Lake Michigan using a ratio-of-means catch rate estimator and new variance estimators, as outlined in Lockwood et al. (in review).

Charter report data

Charter fishery information is generally obtained from harvest reports filed by licensed charter captains to their respective state. Wisconsin initiated a mandatory reporting system in 1974, although because of early underreporting these reports were not considered to be reliable until 1976 (Hansen et al. 1990). Illinois charter boat reporting began in 1976. In Indiana, charter fishery information is sampled in the creel. Charter boat reporting for the Michigan waters began in 1990. Prior to 1990, the Michigan charter fishery information was sampled in the creel.

Harvest Ratio

Fundamental to management is knowing the percentage of stocked fish that are harvested by the fishery. This harvest ratio is defined as the ratio of total number harvested to the total number stocked (Hansen et al. 1990). To estimate a harvest ratio, I calculated an annual harvest age composition for chinook salmon aged by the Michigan creel survey. I applied these age compositions to the lake-wide harvest to estimate year-class harvest for the 1985 to 1992 year classes. I assumed the Michigan age composition applied to the lake-wide population, which seemed reasonable, based on similar length-frequency data from the Wisconsin and Michigan creel surveys. In addition, coded wire tag studies suggest that the chinook salmon population is highly mixed throughout the lake (Bence et al. 1996). I included up to the 1992 year class because the 1993 year class had not been completely harvested by the fishery in 1996.

Lake Regions

I divided the lake into seven distinct regions for a spatial analysis of the chinook salmon fishery (Figure 1). These regions follow statistical district boundaries (Smith et al. 1961), where aggregates of two or more statistical districts constitute a lake region. The Green Bay region includes statistical districts WM-1 and WM-2 from the Wisconsin waters of Green Bay, and MM-1 from the Michigan waters of Green Bay. The Northern region includes Michigan statistical districts MM-2, MM-3, and MM-4 (Grand Traverse Bay). The Northwestern region includes Wisconsin statistical districts WM-3 and WM-4 along the eastern shore of the Door Peninsula. The Northeastern region includes Michigan statistical districts MM-5 and MM-6. The Southwestern region includes Wisconsin statistical districts WM-5 and WM-6. The Southeastern region includes Michigan statistical districts MM-7 and MM-8. The Illinois-Indiana region includes all waters within Illinois and Indiana state boundaries.

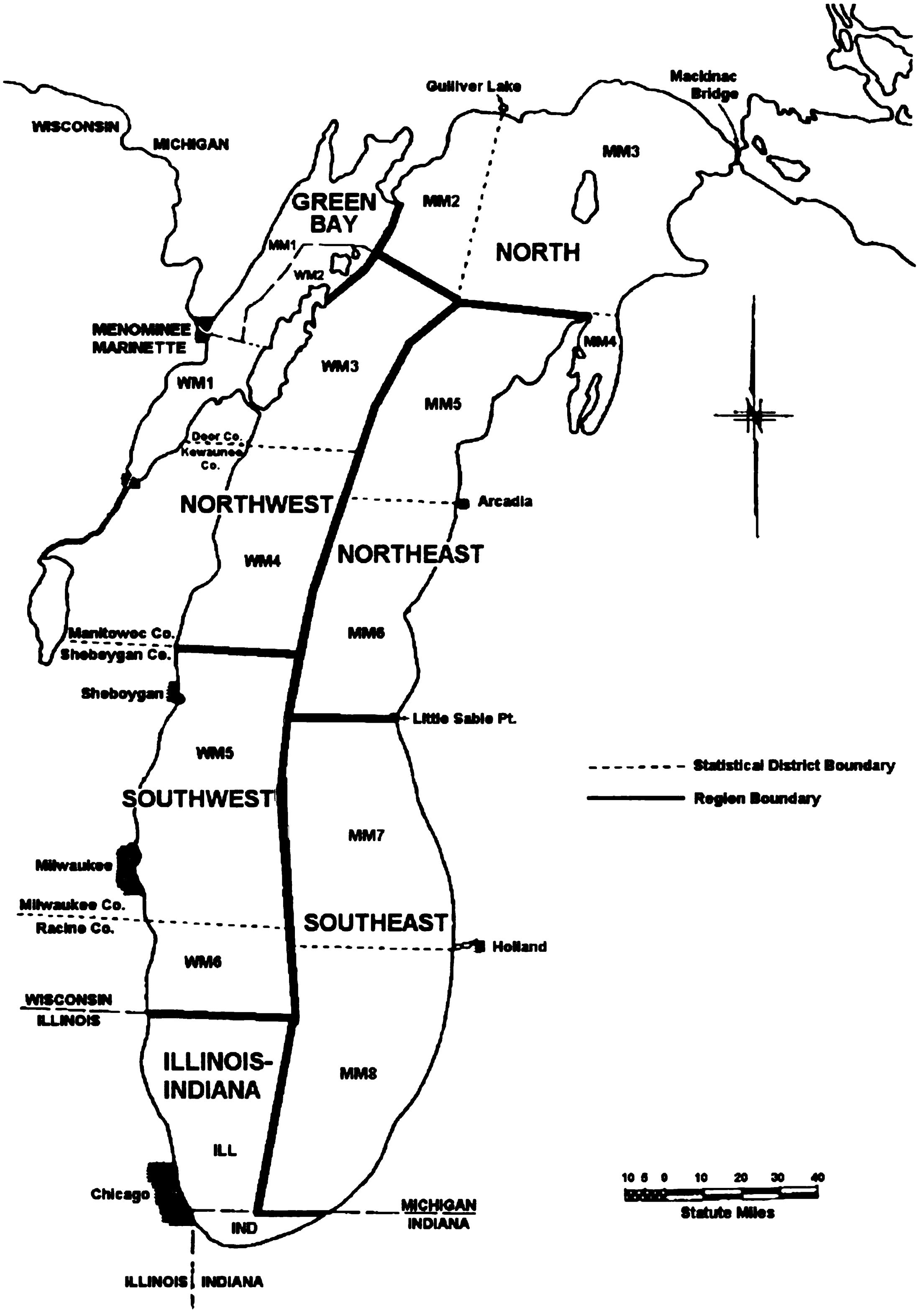

Figure 1. Map of Lake Michigan divided into 7 regions: Green Bay, North, Northwest, Northeast, Southwest, Southeast, and Illinois-Indiana.

Results

Stocking History

Lake-wide stocking of salmonines in Lake Michigan has been presented elsewhere (Keller et al. 1990; Holey 1996). I review the lake-wide stocking history of salmonines in Lake Michigan here because past work has not always given information on all life stages and all years stocked, and because there are inconsistencies in stocking summaries derived from various sources. The procedure used to ensure that the stocking summary presented here is as accurate as possible is described in the Methods. While the trends presented are quite similar to other presentations, details do differ, and these differences become more important when stocking is considered for sub-regions of the lake.

Chinook salmon have historically dominated the stocking program. They are stocked almost entirely as spring fingerlings. Stocking levels increased annually from 900,000 in 1967 to 6 million in 1980 (Figure 2). From 1980 to 1996, stocking fluctuated around 6 million fingerlings with peak years in 1984 (7.7 million) and 1989 (7.9 million).

Significant numbers of lake trout were stocked into Lake Michigan beginning with 1.3 million yearlings in 1965, although 292,000 yearlings were stocked from 1959 to 1962 (Figure 2). Annual stocking of yearlings increased annually to 2.5 million in 1980. Stocking of yearlings has ranged from 1.1 million to 2.8 million from 1981 to 1996. Relatively few fingerlings were stocked in comparison to yearlings in the 1960s and 1970s. Fingerling and fry stocking contributed from 10% to 63% of the total number

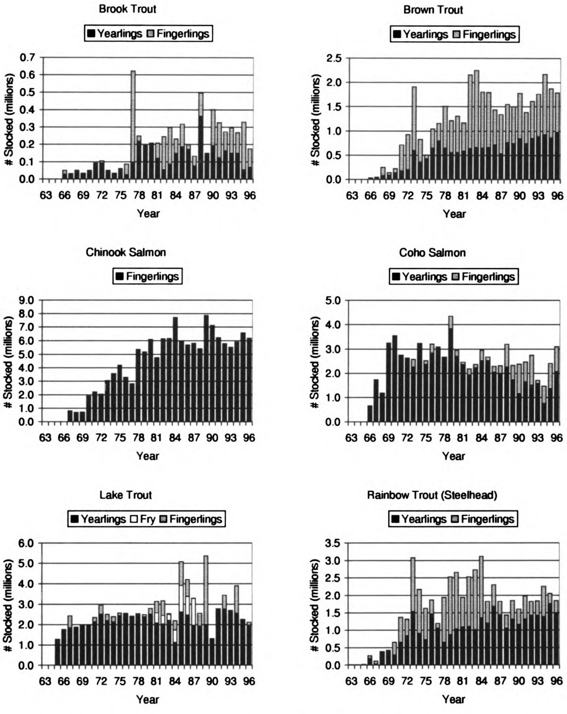

Figure 2. Lake Michigan stocking levels for six species of salmonines from 1963 to 1996.

stocked in the 1980s, and fry have not been stocked since 1987. Total stocking peaked at 5.4 million fish in 1989.

Coho salmon stocking began in 1966 and exceeded 3 million by 1969 (Figure 2). From 1969 to 1996, coho stocking declined from 3.5 million to 2.5 million with a peak year in 1979 (4.4 million). Coho have usually been stocked as yearlings, although the proportion of fingerlings stocked has increased from 1987 to 1996.

Annual rainbow trout (steelhead) stocking levels increased annually from 1963 to 1973, reaching a peak in 1973 at 3 million fish (Figure 2). Stocking fluctuated between 1.2 million and 3.2 million fish from 1974 to 1984. From 1985 to 1996, stocking has been relatively consistent, ranging from 1.5 to 2 million fish. The stocking ratio of yearlings to fingerlings was roughly 1:1 from 1970 to 1984. Since 1985, stocking has been composed of roughly 75% yearlings.

Brown trout stocking began in 1966 and increased to 2 million fish by 1973 (Figure 2). Stocking fluctuated between 500,000 and 1.5 million fish from 1974 to 1981. From 1982 to the present, annual stocking levels have fluctuated between 1.5 and 2 million fish. Brown trout are stocked both as fingerlings and as yearlings.

Brook trout are stocked primarily in Wisconsin waters as both fingerlings and as yearlings, although they were occasionally stocked in Michigan waters until 1990, and in Illinois until 1980. Fewer than 100,000 brook trout were stocked annually from 1966 to 1976 (Figure 2). In 1977, an additional 500,000 fingerlings were stocked in Wisconsin for a total of 623,000 – the most of any year. Stocking levels fluctuated between 200,000 and 300,000 from 1978 to 1986, and between 100,000 and 500,000 from 1987 to 1989. Stocking levels have been declining from 1990 to 1996.

Salmonine Fishery Lake-wide Trends

Sport fishery effort in Lake Michigan declined from 1986 to 1996. Total effort declined by 54%, from 14.1 million angler-hours in 1986 to 6.5 million angler-hours in 1996 (Figure 3). Salmonine effort comprised 61% of the total fishery effort in 1986, but fell to 41% in 1992 before returning to 49% in 1996. Salmonine effort declined by 63% from 8.6 million angler-hours in 1986 to 3.2 million angler-hours in 1992. Salmonine effort has been stable at 3.2 million angler-hours from 1992 to 1996.

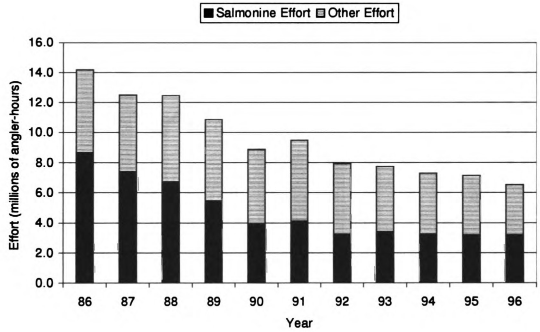

Figure 3. Total effort and salmonine effort (in millions of angler-hours), from the Lake Michigan sport fishery, 1986 to 1996. Other effort includes effort not directed at salmonines, as well as effort reported by the charter fishery.

Harvest of salmonines declined by 53% from 1.8 million salmonines in 1986 to 855,000 in 1990 (Figure 4). From 1990 to 1996, salmonine harvest has been relatively consistent at 800,000, with a low harvest occurring in 1992 at 746,000 salmonines. Targeted salmonine harvest rate (targeted salmonine harvest per salmonine angler-hour) fluctuated between 0.12 and 0.16 from 1986 to 1990 (Figure 4). Harvest rate has been increasing from 1990 to a period high of 0.19 in 1996.

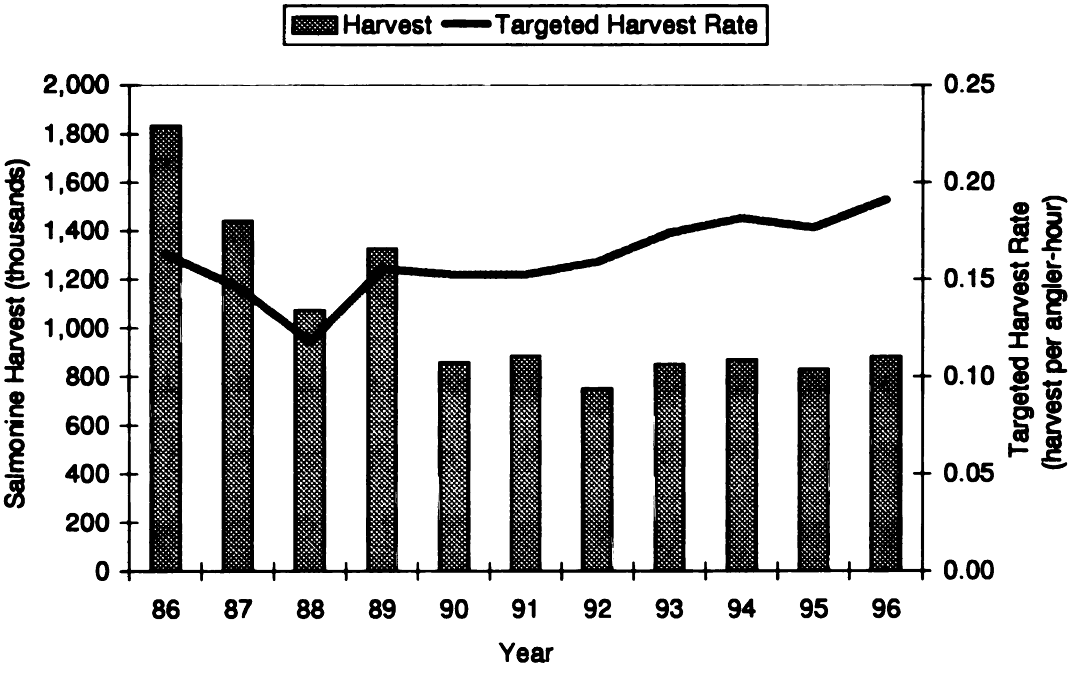

Figure 4. Salmonine total harvest (in thousands of fish) and targeted harvest rate of salmonines from the Lake Michigan sport fishery, 1986-1996. See Methods for a description of targeted harvest rate.

Lake-wide harvest of coho salmon peaked in 1989 at 407,000 and declined to 155,000 in 1991. Harvest levels from 1992 to 1996 ranged from 181,000 to 295,000 with an average of 237,000. Contribution of coho salmon harvest to the total salmonine harvest increased from 18% in 1986 to 35% in 1993.

Lake trout are generally not preferred by anglers, but are relied upon when fishing for other salmonines is poor (Lange et al. 1995). Lake trout harvest comprised 13% to 27% of the salmonine harvest between 1986 and 1996. Peak harvest was in 1989 at 347,000 while 1996 was the lowest harvest year at 115,000.

Rainbow trout harvest was limited to a stream fishery in the mid- to late-1980s. In 1986, the lake harvest of rainbow trout was 68,000, less than 5% of the salmonine harvest. An offshore fishery developed for rainbow trout as anglers learned to target rainbow trout along surface temperature breaks, and harvest increased to a peak of 172,000 in 1993, comprising 20% of the salmonine harvest. Harvest declined to 142,000 in 1996.

Brown trout harvest has accounted for 6% to 13% of salmonine harvest from 1986 to 1996. Harvest declined from 171,000 in 1986 to 73,000 in 1988. Harvest has fluctuated between 63,000 and 110,000 from 1987 to 1996. Most brown trout are harvested in Wisconsin and Michigan.

Brook trout harvest has historically accounted for less than 1% of lake-wide salmonine harvest. Most brook trout harvest is concentrated in Wisconsin, although a small fraction is harvested in Michigan. Harvest has ranged from 500 to 6,000 from 1986 to 1996.

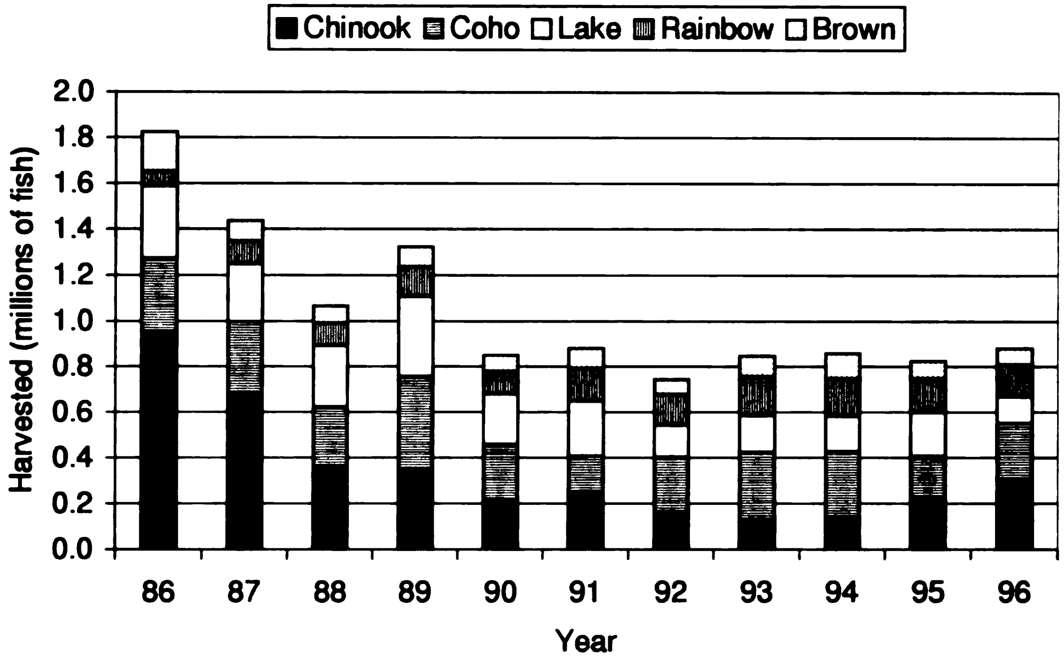

Figure 5. Lake-wide salmonine harvest (in millions of fish) by species for the Lake Michigan sport fishery, 1986-1996. (Chinook = chinook salmon, Coho = coho salmon, Lake = lake trout, Rainbow = rainbow trout and steelhead, Brown = brown trout)

Chinook salmon fishery lake-wide and regional trends

In the subsections that follow I present detailed information on temporal trends in harvest, effort, and catch rate for chinook salmon for each region of Lake Michigan. These detailed results show the following general patterns. First, there were substantial differences in how the overall collapse of the chinook salmon fishery unfolded. Most notably, the decline was greater on the eastern (Michigan) shore in comparison with the western (Wisconsin) shore, with the greatest decline in the southeast. This generalization applied to harvest (Figure 7), harvest rate (Figure 8), and harvest ratio (percent of a stocked year class harvested (Figure 10), but less so to the amount of fishing effort on salmonines (Figure 6). These results suggest some spatial changes over time in either the distribution or survival of chinook salmon. I return to this topic in the Discussion. In addition, comparisons of stocking, harvest, and harvest ratio provided no evidence that regional in-lake harvest was closely tied to regional stocking numbers.

Regional trends in salmonine effort for the sport fishery

Trends in salmonine effort for each region of Lake Michigan generally followed a lake-wide trend of declining effort in the late 1980's, followed by a consistently low level of effort in the early to mid-1990's. The major differences between regions were the years in which the declines actually began and ended, and the overall extent of the declines (Figure 6).

Salmonine effort in Green Bay increased from 1986 to 1988 before declining by 69% from 384,000 angler-hours in 1988 to 119,000 angler-hours in 1996. Effort was relatively consistent from 1992 to 1996. In comparison to the lake-wide salmonine effort, effort in Green Bay contributed 3-7% of the lake-wide total from 1986 to 1996.

Salmonine effort in the Northern region was at a period-low level in 1986 in contrast to a period-high level lake-wide. Effort peaked in 1987 at 245,000 (± 20,000) angler-hours and fluctuated between 157,000 (± 16,000) and 194,000 (± 17,000) angler-hours from 1988 to 1993. Effort has been declining from 194,000 (± 17,000) in 1991 to 119,000 (± 6,900) in 1996. Similar to Green Bay, effort in the northern region contributed between 3% and 6% of the lake-wide effort from 1987 to 1996.

Salmonine effort in the Northwest region declined by 55% from 984,000 angler-hours in 1986 to 439,000 angler-hours in 1990, similar to the lake-wide rate of decline of 53% over the same years. Effort from 1990 to 1996 has been relatively stable at 400,000 to 450,000 angler-hours. Effort in the northwest comprised 9-14% of the lake-wide total from 1986 to 1996.

The high rate of decline of salmonine effort in the Northeast region was second only to the Southeast, declining by 69% from 1.6 million (± 172,000) angler-hours in 1986 to 510,000 (± 33,000) angler-hours in 1992. Period-low salmonine effort occurred in 1995 at 424,000 (± 34,000) angler-hours. Effort in the northeast comprised 13-23% of the lake-wide total from 1986 to 1996.

Salmonine effort in the Southwest did not begin to decline until 1988, and declined by 62% from 1.4 million angler-hours in 1987 to 542,000 angler-hours in 1990 (Figure 6). Effort remained low from 1990 to 1993, and increased slightly to 620,000 angler-hours from 1994 to 1996. Effort in the southwest comprised 13-20% of the lake-wide total from 1986 to 1996.

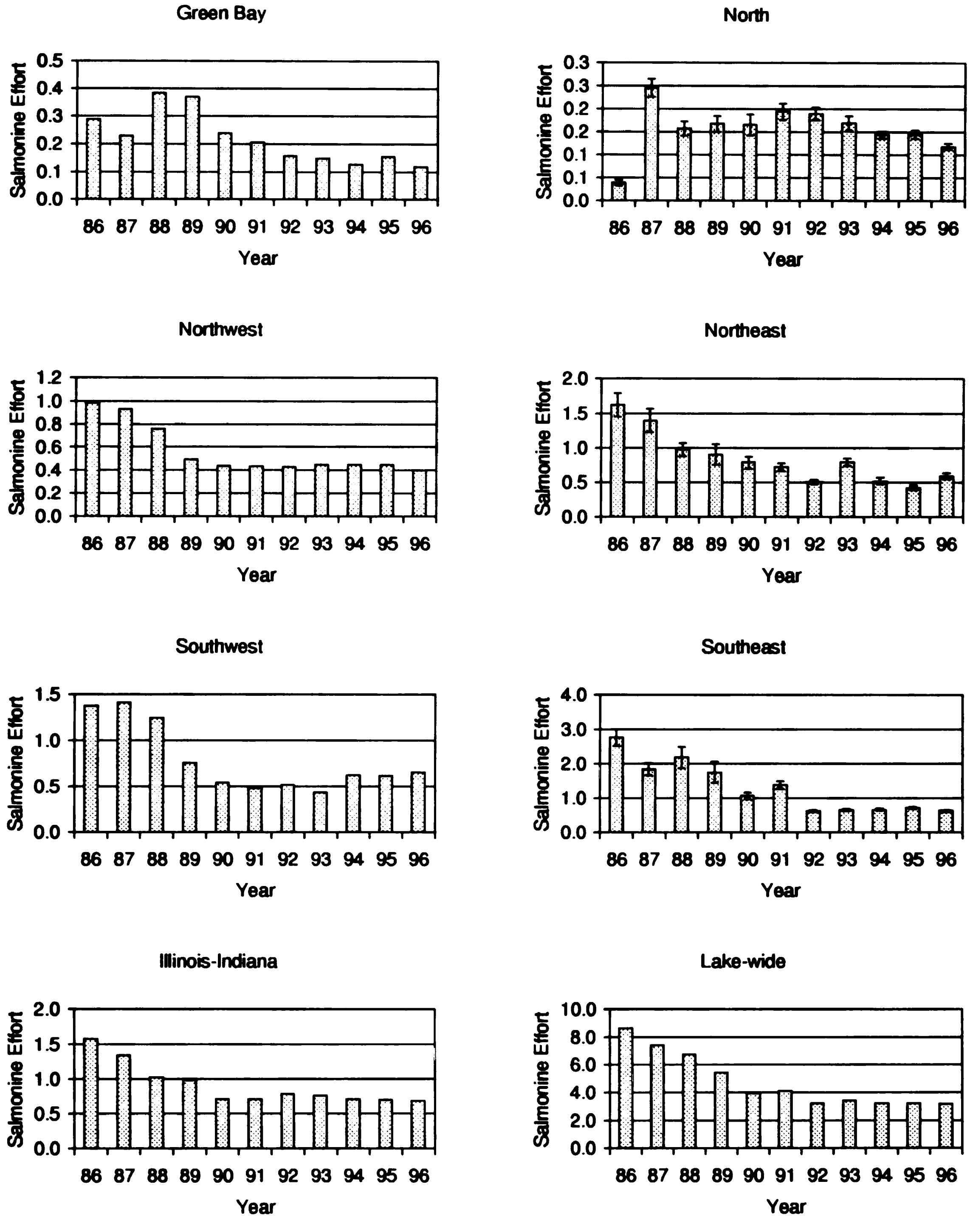

Figure 6. Salmonine effort (in millions of angler-hours) from the Lake Michigan sport fishery, 1986 to 1996. Standard error bars are shown for regions within Michigan's waters only. See Figure 1 for a definition of lake regions.

The greatest declines in Lake Michigan salmonine effort occurred in the southeast region. Salmonine effort declined by 77% from a peak of 2.75 million (± 241,000) angler-hours in 1986 to a period low level of 621,000 (± 38,000) angler-hours in 1992. Effort has remained below 715,000 angler-hours from 1992 to 1996 (Figure 6). Effort in the southeast once comprised 32% of the lake-wide total in 1986, but declined to 19% by 1993. Salmonine effort in the Illinois-Indiana region is large relative to its lake area, due primarily to the high human population density along almost it's entire shoreline. In 1992, 1994, and 1996, this region reported more salmonine effort than any other region in the lake (Figure 6). Salmonine effort declined by 55% from 1.6 million angler-hours in 1986 to 706,000 angler-hours in 1990. Effort has been relatively stable from 1990 to 1996 at 682,000 to 782,000 angler-hours. The relative contribution of effort in the Illinois-Indiana region to the lake-wide total increased from 15-18% from 1986 to 1991, to 21-24% from 1992 to 1996.

Chinook salmon harvest

The decline in salmonine harvest from 1986 to 1988 was driven by declines in chinook salmon harvest (Figure 5). In 1986, chinook salmon harvest comprised more than 50% of the total salmonine harvest. By 1993, chinook salmon comprised only 16% of the salmonine harvest. Lake-wide chinook salmon harvest declined by 86% from 950,000 in 1986 to 132,000 in 1993 (Figure 7). Harvest increased from 226,000 in 1994 to 304,000 in 1996, but remains less than one-third of the peak harvest in 1986. Trends in chinook salmon harvest differ across regions and do not follow a general lake-wide trend. In general, harvest declines were greater in the eastern regions of the lake than in the western regions.

Chinook salmon harvest in Green Bay increased from 27,000 in 1986 to 42,000 in 1989, while the lake-wide harvest declined over the same period. Harvest declined by 46% from 1989 to 1990, and period-low harvest of 6,000 occurred in 1993 for an overall decline of 86% from 1989 to 1993. Harvest in Green Bay was 3% of the lake-wide total in 1986, increased to 12% in 1989, and has fluctuated between 3 and 10% from 1990 to 1996.

Only a small fraction of the lake-wide salmonine fishery is contained in the Northern region of the lake, probably because the region is less densely populated, fewer salmonines are stocked there, and because tribal fisheries and lake trout refuges limit sport fishing effort. Relatively few chinook salmon are harvested in the northern waters of Lake Michigan. From 1986 to 1996, harvest in the northern waters contributed 1-6% of the lake-wide harvest. Still, declines in harvest generally followed the lake-wide trend, with a peak in harvest of 23,000 (± 3,700) in 1987 and a low harvest of 2,400 (± 300) in 1994 for an overall decline of 90% (Figure 7).

Chinook salmon harvest in the northwest region contributed 11% to 32% of the lake-wide harvest from 1986-1996 (Figure 7). Peak harvests were 102,000 in 1986 and 113,000 in 1987. Harvest from 1988 to 1996 was lower than previous years, with additional peak years in 1989 and 1996. Period-low harvest occurred at 42,000 in 1992 for an overall decline of 63% from 1987 to 1992. Harvest has been increasing annually from 1993 to 1996.

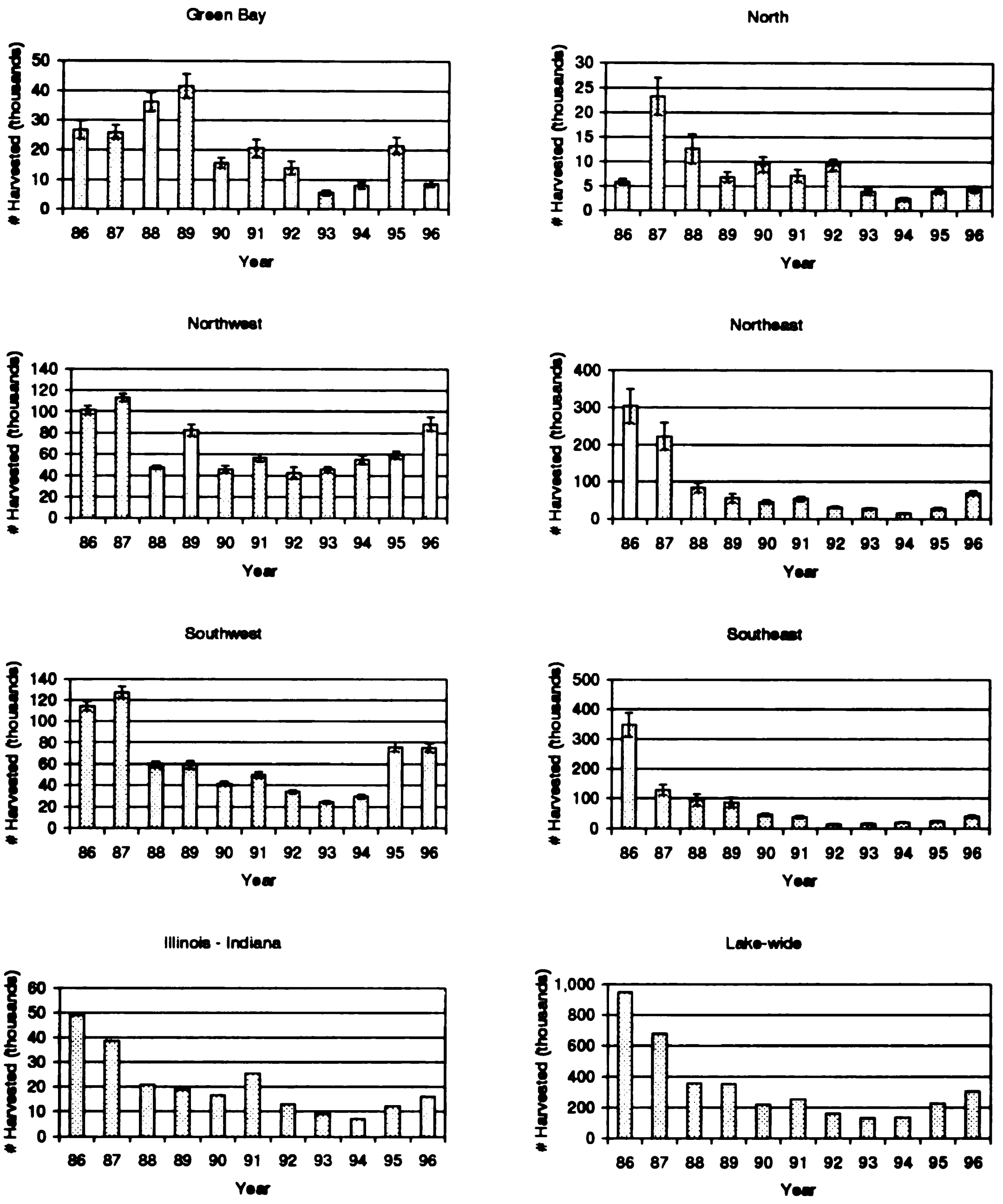

Figure 7. Chinook salmon harvest from the Lake Michigan sport fishery, by lake region, 1986 to 1996. Standard error bars are shown for Michigan and Wisconsin harvest only. See Figure 1 for a definition of the lake regions.

Second only to the southeast, chinook salmon harvest in the northeast region declined more than any other region. Harvest in the northeast region peaked in 1986 at 304,000 (± 46,000) and declined by 95% from 1986 to 15,000 (± 1,100) in 1994 (Figure 7). Harvest increased to 70,000 in 1996, the highest level of harvest since 1988.

Chinook salmon harvest in the southwest region increased from 115,000 in 1986 to 128,000 in 1987 before declining by 53% in 1988 (Figure 7). Harvest continued to decline to a period low of 24,000 in 1993 - an overall decline of 81% between 1987 and 1993. Harvest increased to 75,000 in 1995 and 1996.

Chinook salmon harvest in the southeast region declined by 63% from a peak of 348,000 (± 41,000) in 1986 to 129,000 (± 19,000) in 1987. Harvest continued to decline to a low of 14,000 (± 1,400) in 1992 - an overall decline of 96% from 1986 to 1992. Harvest increased from 16,000 (± 1,600) in 1993 to 40,000 (± 3,100) in 1996 (Figure 7). Along with declines in salmonine effort, chinook salmon harvest declined more in the southeast than any other region of the lake.

Chinook salmon harvest from the Illinois and Indiana waters followed a decline similar to the lake-wide trend from 1986 to 1994 (Figure 7). Peak harvest occurred in 1986 at 49,000 and declined by 85% to 7,000 in 1994. Harvest has increased from 1994 to 1996. From 1986 to 1991, contribution of harvest from the Illinois and Indiana waters to the lake-wide harvest increased from 5% to 10% before declining to 5% again in 1996.

Chinook salmon targeted harvest rates as an index of abundance

Lake-wide targeted harvest rates (targeted chinook salmon harvest per salmonine angler-hour) of chinook salmon suggest that relative abundance declined from 1986 to 1993, and increased from 1994 to 1996 (Figure 8). Harvest rate declined concurrently with declines in harvest, from 0.087 in 1986 to 0.027 in 1993, and increased to 0.064 by 1996. There were regional differences in harvest rate trends, namely, declines occurred in the north and eastern regions of the lake, while declines in the western regions were not as severe and in some cases harvest rate actually increased. Because much of the fishery is concentrated in the eastern regions, these regions had the most influence on the lake-wide harvest rate trend. Regional differences in harvest rate trends suggest a change in the spatial distribution of chinook salmon rather than simply a decline in lake-wide abundance.

Targeted harvest rates in Green Bay ranged from 0.030 to 0.083 from 1986 to 1996, but do not show a declining trend, as peak rates occurred in 1989, 1991, and 1995 (Figure 8). Harvest rates in the northern region declined by 82% from 0.086 (±0.017) in 1987 to 0.016 (±0.002) in 1994. Harvest rates in the northwest showed the largest decline from 1987 to 1988 but have fluctuated between 0.046 and 0.075 from 1989 to 1995. Harvest rates increased from 1992 to 1996, with a period-high harvest rate of 0.11 in 1996. Harvest rates in the northeast similarly declined from 0.13 (±0.024) in 1986 to 0.024 (±0.003) in 1994. Harvest rates increased in 1995 and 1996, surpassing the 1987 level. In the southwest region, harvest rates peaked at 0.061 in 1987 before declining to a low of 0.020 in 1994 – a 70% decline. However, by 1995, harvest rates returned to 1986-1987 levels. Harvest rate in the southeast declined by 82% from 0.12 (±0.018) in 1986 to 0.021 (±0.003) in 1992. By 1996, harvest rate had returned to the 1987 level of 0.063 (± 0.006). In the Illinois-Indiana region, harvest rates declined from 0.031 in 1986 to 0.010 in 1994 before increasing to 0.024 in 1996.

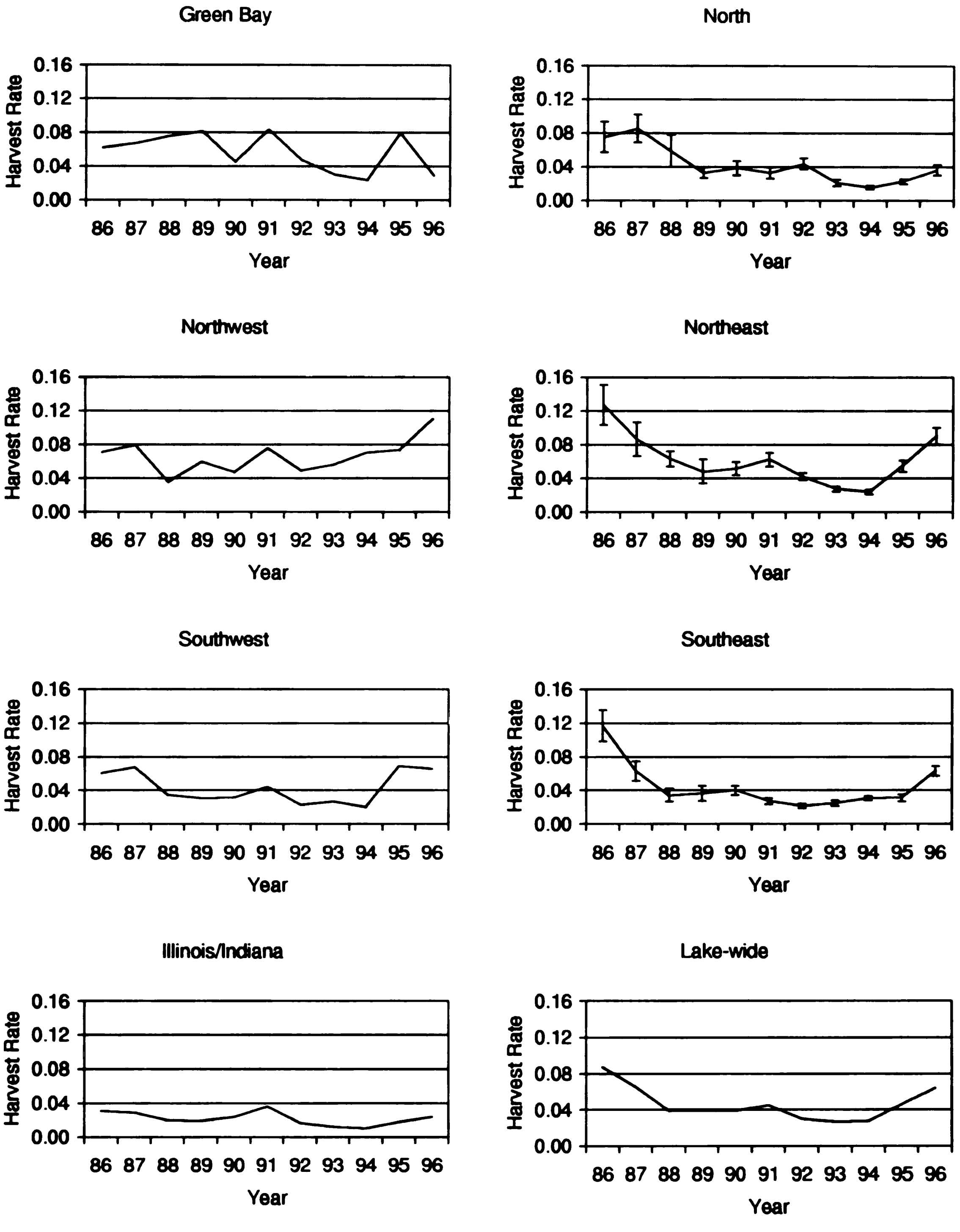

Figure 8. Chinook salmon targeted harvest rates (targeted harvest per salmonine angler-hour), by lake region, for the Lake Michigan sport fishery, 1986-1996. Standard error bars are shown only for Michigan (see Methods). See Figure 1 for a definition of lake regions.

Regional year class stocking, harvest, and harvest ratio (% return)

From 1985 to 1988, lake-wide stocking levels fluctuated by 10% from 5.4 million to 5.9 million. Harvest of those year classes, however, declined by 55% from 464,000 for the 1985 year class to 209,000 for the 1988 year class (Figure 9). Stocking increased to an all-time high of 7.85 million in 1989 while the harvest of that year class was 185,000 and the harvest ratio (percent of stocked fish harvested by the fishery) fell below 3%. Harvest ratio remained below 3% for the 1990 to 1992 year classes (Figure 10). All regions of Lake Michigan experienced declining year class harvest from the 1985 year class to the 1992 year class. Additionally, changes in regional year class harvest do not appear to have been affected by local (within region) changes in stocking. If year class harvest was affected by stocking levels, it was masked by the influence of changes in stocking outside the local region, which further suggests that chinook salmon spatial distribution was changing, and that this change had an effect on the fishery.

Year-class harvest in Green Bay declined from the 1985 to the 1988 year classes concurrent with declines in stocking (Figure 9). Stocking was highest in 1989 before declining again through 1992. Increased stocking levels in 1989 and 1990 did not improve year class harvest. Harvest ratio for the 1985 to 1988 year classes was relatively constant at 5.1-5.7%, and dropped below 3% for the 1989 to 1992 year classes (Figure 10). The low harvest ratios for these four year classes were comparable to the lake-wide values.

Harvest in the northern region was highest for the 1985 year class, and declined for the 1986 and 1987 year classes (Figure 9). Year class harvest was relatively consistent for the 1987 to 1991 year classes before declining again for the 1992 year class. Stocking increased from 1985 to 1989 before declining slightly from 1990 to 1992. Harvest ratio showed a similar trend to year class harvest. Harvest ratios in the North peaked at 2.75% for the 1985 year class and declined to 0.5% for the 1992 year class (Figure 10).

Year class harvest in the northwest region declined by 31% from 72,000 for the 1985 year class to 50,000 for the 1987 year class, despite consistent stocking levels of 1.1 million (Figure 9). Harvest has been relatively consistent for the 1987 to 1992 year classes at 42,000 to 53,000. Stocking levels were reduced in 1988 to 728,000 but peaked in 1989 at 1.2 million fingerlings before declining again from 1990 to 1992. Harvest ratio ranged from 4.96 to 6.42 from the 1985 year class to the 1988 year class, but declined to 3.63 for the 1989 year class. The harvest ratio increased for the 1990 to 1992 year classes, reaching a peak of 10.6 for the 1992 year class (Figure 10).

Approximately 800,000 chinook salmon were stocked annually in the northeast from 1985 to 1987, while harvest of those three year classes declined by 65% from 130,000 to 45,000 (Figure 9). Stocking increased each year from 1988 to 1990, while year class harvest remained consistently below 50,000. Harvest ratio for the 1985 year class exceeded 15%, and declined for each subsequent year-class to a low of 1.8% for the 1992 year class (Figure 10).

Year class harvest in the southwest declined by 61% from 78,000 for the 1985 year class to 31,000 for the 1991 year class (Figure 9). Stocking declined by 59% from 1.1 million in 1985 to 455,000 in 1988, concurrent with the decline in year-class harvest. Increases in annual stocking of 1.1 million in 1989 and 1990 did not cause an increase in year-class harvest. Harvest ratio has fluctuated from 3.2% for the 1990 year class to 8.6% for the 1988 year class (Figure 10).

Harvest in the southeast declined by 85% from 115,000 for the 1985 year class to 17,000 for the 1991 year class (Figure 9). Harvest ratio followed the same trend as year class harvest, declining by 89% from 9.3% to 1.0% from the 1985 year class to the 1991 year class (Figure 10). Stocking from 1985 to 1988 was relatively constant at 1.3 million. Stocking increased to 1.8 million in 1989 and declined to 1.5 million in 1992. Changes in stocking did not increase year class harvest.

Harvest in the Illinois-Indiana region declined by 42% from 26,000 to 15,000 from the 1985 year class to the 1987 year class, despite increases in stocking by 54% from 1985 to 1987 (Figure 9). Harvest ratio similarly declined by 63% from 4.7% to 1.8% over the same period (Figure 10). Harvest ratio has been consistently low at 1 to 2% from the 1987 to the 1992 year class.

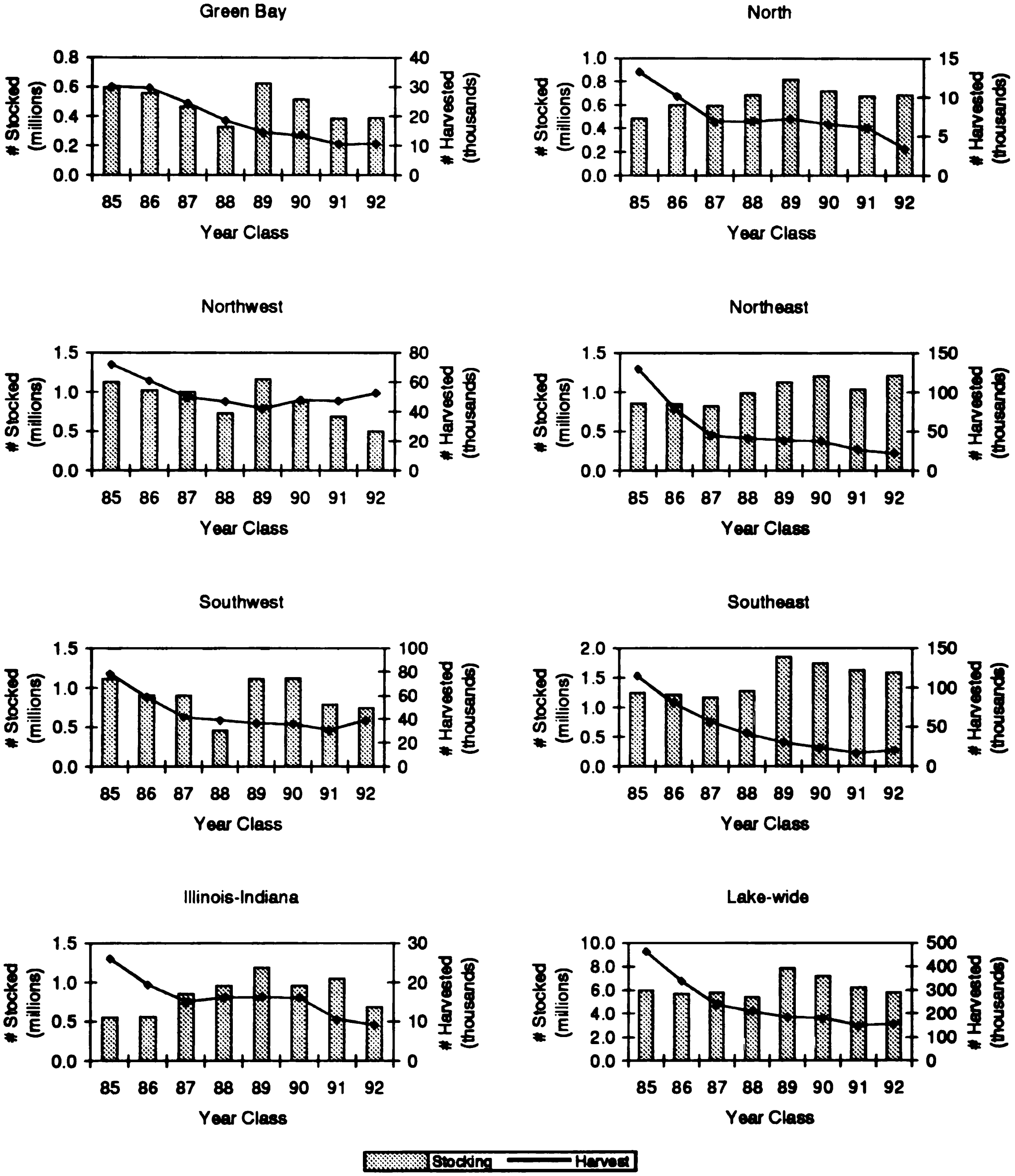

Figure 9. Chinook salmon stocking and harvest, by year-class and region, for the Lake Michigan sport fishery. See Figure 1 for a definition of lake regions.

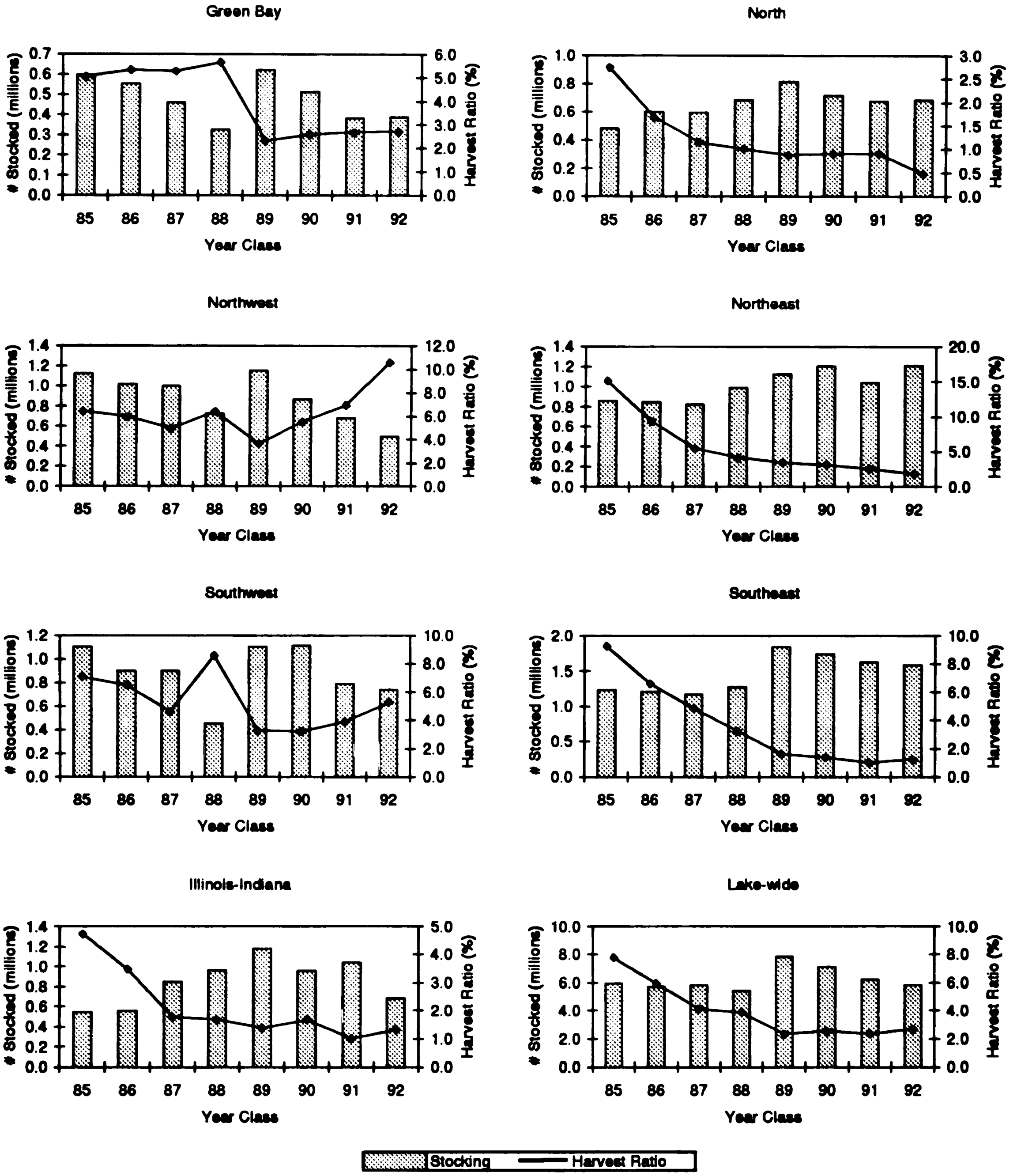

Figure 10. Chinook salmon stocking and harvest ratio, by year-class and region, for the Lake Michigan sport fishery. See Figure 1 for a definition of lake regions.

Discussion

The Lake Michigan salmonine fishery has changed dramatically from 1986 to 1996. Lake-wide effort declined from 1989 to 1992 and has been consistently low from 1992 to 1996. Salmonine harvest declined from 1986 to 1990, and remained relatively stable from 1990 to 1996. An increase in the targeted salmonine harvest rate from 1990 to 1996 is an indication that the salmonine fishery was not completely dependent upon the success of the chinook salmon harvest. Anglers shifted their efforts towards other salmonines and maintained high harvest rates. The harvest rate of 0.14 in 1996 was higher than the peak harvest years of 1986 and 1987. Hansen et al. (1990) reported a salmonine harvest rate exceeding 0.15 from 1982 to 1985 for the Wisconsin waters, suggesting that the lake-wide fishery may have peaked prior to 1986.

The question remains as to why the chinook salmon fishery collapsed in the early 1990s. Keller et al. (1990) suggest that the collapse was driven by changes in the geographical distribution of chinook salmon, poor year class survival, and increased mortality due to disease. This study provides information on the extent and location of the declines in the fishery as well as some additional insight into the causes of the fishery collapse. I believe that declines in the Lake Michigan chinook salmon fishery were the result of changes in fishing effort, natural mortality, and the spatial distribution of the salmon.

Declines in salmonine effort from 1986 to 1996 were a lake-wide phenomenon with relatively little difference in the rate of decline across lake regions. Salmonine harvest likely declined as a result of declining effort, although rates of harvest decline were not consistent across species. Chinook salmon harvest declined far more than harvest of any other salmonine, indicating that chinook salmon harvest was driven by more than simply changes in effort.

While following trends in salmonine effort eliminates bias associated with effort for yellow perch or other species, changes in salmonine effort may not accurately track changes in effort targeted at chinook salmon. Anglers contend that they use different fishing methods to target lake trout, rainbow trout, and salmon by fishing different depths, fishing with different lures or colors, or by fishing along temperature breaks (Bence and Smith in press; personal observation). Anglers increasingly targeted chinook salmon in the early 1980's, but shifted their effort towards other salmonines when chinook salmon fishing was poor (Bence and Smith in press).

Further analysis suggests that salmonine effort shifted away from chinook salmon and towards other species during the late 1980's. In 1986, 10% of angling parties interviewed in Michigan's boat fishery indicated that they were specifically targeting chinook salmon (Jerry Rakoczy, Michigan DNR, unpublished data). By 1993, only 1% of anglers were targeting chinook salmon. Similarly, the percentage of boat anglers that were specifically targeting salmon was 26% in 1987, and declined to 8% by 1992. In contrast, the percentage of boat anglers targeting trout in general increased from 1% in 1986 to 8% in 1994. Boat anglers may have also become less specific as the fishery changed in the 1980s and 1990s. The percentage of boat anglers targeting salmon *and* trout increased from 24% in 1986 to 34% in 1991. Finally, the percentage of anglers that indicated they were not targeting anything at all increased from 3% in 1986 to 12% in 1992.

Because of the popularity of chinook salmon in Lake Michigan, and because they are the most important salmonine in terms of numbers stocked and harvested, declines in harvest rates for chinook salmon probably contributed to the initial cause of the decline in salmonine effort from 1986 to 1988 (Bence and Smith in press). Successful anglers were able to redirect their effort towards other salmonines, while unsuccessful anglers reduced their fishing effort or left the fishery altogether. The result has been an increasing salmonine harvest rate from 1988 to 1996 (Figure 4).

Increasing public knowledge of contaminants in Great Lakes fish and fish consumption advisory publications may have played a role in declines in effort. In 1989, the National Wildlife Federation (NWF) published a controversial Lake Michigan fish consumption report that had an immediate impact on the fishery and caused a cascade of media coverage (Associated Press 1989; Campbell 1989; NWF 1989). Reports of dead chinook salmon on Lake Michigan beaches from 1987 to 1989 could have also served as a message to the angling public that the fish in Lake Michigan were not healthy to eat and therefore not worth the effort and money required to catch them. Consumption issues are unlikely to be the cause of the continued low levels of fishery effort. A 1996 survey of Great Lakes anglers revealed that concerns about fish contamination was the least likely reason for low fishery effort. A lack of free time was cited as the most likely reason, followed by low catch rates (Michigan Sea Grant 1998).

Another explanation for declines in fishing effort is that the pattern on Lake Michigan reflects a trend that goes beyond what is happening on either Lake Michigan or the Great Lakes in general. It could reflect part of a national trend for the public to spend less time in activities such as fishing and hunting (Bence and Smith in press).

Poor year class survival has been implicated as one of the causes of the poor chinook salmon fishery in the late 1980's (Keller et al. 1990). Poor returns to the sport fishery and to the weirs are evidence of poor year class survival beginning with the 1984 year class, although the causes are unknown. Most likely, though, the poor survival was a result of in-lake processes and was not caused by changes in the condition of the hatchery product (Keller et al. 1990). Since no marked changes in growth rates were observed for chinook salmon prior to 1985 and the onset of BKD (Wesley 1996), it is likely that poor survival prior to 1985 was due to early life mortality. Higher mortality rates probably affected the older age classes after 1985 because most chinook that washed up on beaches in the late 1980's were age 2 or older (Nelson and Hnath 1990; Johnson and Hnath 1991). Further, growth rates of older chinook salmon significantly increased after the BKD outbreak than before the outbreak, suggesting that density-related stress immediately prior to the BKD outbreak may have slowed growth rates and triggered increased mortality (Wesley 1996). Finally, the age structure of the harvest in Michigan's waters shifted towards younger age classes in the late 1980's (see Chapter 3).

Quantifying these increased mortality rates has been difficult. Because BKD was implicated as the ultimate cause of death for chinook salmon on beaches in the late 1980's, managers have monitored the incidence of BKD in an attempt to monitor natural mortality rates. Incidence of BKD is monitored in chinook salmon returning to the weirs and in fishery-independent surveys. Fish are examined for clinical signs of disease, and blood samples are tested specifically for BKD (Clark 1996). While this monitoring is intended to provide an index of in-lake BKD mortality, the statistic "percent positive with BKD" is difficult to interpret because it could mean one of two things. First, a decrease in BKD incidence could reflect in-lake decreases in BKD mortality, which assumes that the sampled fish are representative of the population. Second, a decrease in BKD incidence could instead reflect in-lake increases in BKD mortality, which assumes that a greater proportion of infected fish die than survive to be tested (Clark 1996). Because of this dichotomy, "percent infection rates" should not be used as the only index of BKD mortality rates (Clark 1996).

Tests for the presence of *Renibacterium salmoninarum*, the causative agent of BKD, at the Strawberry Creek weir in Sturgeon Bay, Wisconsin, have shown a decline in the percentage of positive chinook salmon from a peak of 67% in 1988 to a low of 2% in 1994 (Marcquenski 1996). Incidence of clinical signs of BKD in chinook salmon returning to Michigan weirs was about 85% in the late 1980s and declined to less than 10% by 1992 (Clark 1996). Clinical signs of BKD returning to the Manistee weir in 1992, however, were greater than 20% and declined to less than 10% in 1995. Visual signs of BKD in chinook salmon collected from a fishery-independent survey from 1990 to 1996 showed a peak level of about 37% and declined to less than 5% in 1996 (Clapp 1997). Laboratory tests for BKD of survey-caught fish in 1996, however, showed greater than 10% incidence. Visual estimates of BKD incidence from surveys were consistently higher than visual estimates from Michigan weirs (Clapp 1997) and could be an indication that fewer BKD-infected fish survive to maturity.

Keller et al. (1990) noted that catch of chinook salmon in 1987 occurred in the northern regions of the lake one month earlier in the season than normal. They suggested that chinook salmon were more evenly distributed throughout the lake than normal due to milder winter temperatures, and that this change in distribution contributed to the poor

1987 chinook salmon fishery. An even distribution of chinook salmon throughout the lake should be reflected by similar trends in regional catch rates. Poor survival would decrease abundance lake-wide, and similar declines in regional catch rates would reflect this. However, catch rates did not decline similarly across all regions, which suggests that chinook salmon were not evenly dispersed but were in fact spatially congregated.

Temperature and food seem to be the two driving factors that influence chinook salmon distribution (Keller et al. 1990; Elliott 1993). Chinook salmon prey primarily upon alewife, bloater, and smelt, but there is debate about whether chinook salmon prefer alewife (Jude et al. 1987), or whether they are opportunistic (Elliott 1993; Rybicki and Clapp 1996). Forage abundance in Lake Michigan varies seasonally and spatially (Brandt et al. 1991). In particular, alewife and rainbow smelt have been more abundant and constitute a larger proportion of the forage abundance in the northern and western waters of the lake. Bloaters are abundant throughout the lake but are dominant in the eastern waters. Regional diets of sport-caught chinook salmon reflect regional forage abundance (Hagar 1984; Toneys 1992; Elliott 1993; Peeters 1993; Rybicki and Clapp 1996).

Alewife spatial distribution in Lake Michigan shifted between 1985 to 1995 (Ann Krause, Michigan State University, unpublished results). Alewives were abundant across western and eastern regions of the lake in the mid-1980's, as indicated in trawl surveys conducted by the Great Lakes Science Center. Abundance then declined in the eastern regions of the lake in the early 1990's as abundance in the western regions increased (Figure 11). Trends in alewife distribution and abundance appear to match trends in chinook salmon harvest and targeted harvest rates (Figure 7 and Figure 8), and suggest that the spatial distribution of chinook salmon changed as the spatial distribution of alewife changed. This is further supported by preliminary survey data which show a correlation between high chinook catch rates and a high proportion of alewives in their stomachs (Dave Clapp, Michigan DNR, personal communication). Earlier studies showed seasonal and spatial differences in chinook diets that corresponded with forage abundance and species composition (Elliott 1993), suggesting that chinook salmon demonstrated a seasonal migration in the spring away from eastern waters and back again in the fall. If chinook salmon prefer alewife as their primary prey, then changes in prey distribution would cause changes in predator distribution and would be reflected in the fishery. Chinook salmon that successfully migrated in order to continue to prey on alewives survived, while those did not follow alewives were forced to prey on other species – namely bloater and rainbow smelt. Chinook salmon that preyed primarily upon species other than alewife may have been more susceptible to nutritional stress and subsequent mortality.

While localized increases in mortality may have been possible, especially in the southeast region of the lake, it is not accurate to think of the lake as consisting of several distinct populations suffering different mortality rates. Chinook salmon that tend to stay in a given area may suffer different mortality rates than fish in other areas, but the fish in each area is a mix of fish that originated from different stocking and spawning locations, and the mix is itself likely to be dynamic as forage abundance changes spatially over time. This highly migratory nature of chinook salmon suggests that changes in spatial distribution are likely to have caused most of the regional differences in how the fishery changed.

Attempts to increase local yields in Lake Michigan by increasing local stocking are likely to lead to frustration. Regional increases in stocking levels did not improve regional year class harvest. This was particularly true for the Northeast and Southeast regions, where year class harvest continued to decline for the 1985 to 1993 year classes despite increases in stocking levels from 1985 to 1992 (Figure 9). During the study period, lake-wide increases in numbers stocked for a year class also did not lead to lake-wide increases in harvest. If anything, lake-wide increases in stocking led to declines in harvest, CPUE, and other measures of fishery success. This is probably due to density dependent processes, which although not proven, is consistent with the data. For example, BKD infection rates are positively related to stocking levels (Clark 1996). Of special importance, the harvest ratio observed for the 1989 through 1992 year classes (about 2.5%) represented a substantial decline over that seen for the 1985 (about 8%). Harvest ratios probably had already declined for the 1985 year class in comparison with earlier cohorts. This year class was impacted by BKD mortality, and the harvest ratios for the 1985 year class calculated for Wisconsin's waters were already substantially below those reported for Wisconsin for the 1969-1982 year classes (Hansen et al. 1990).

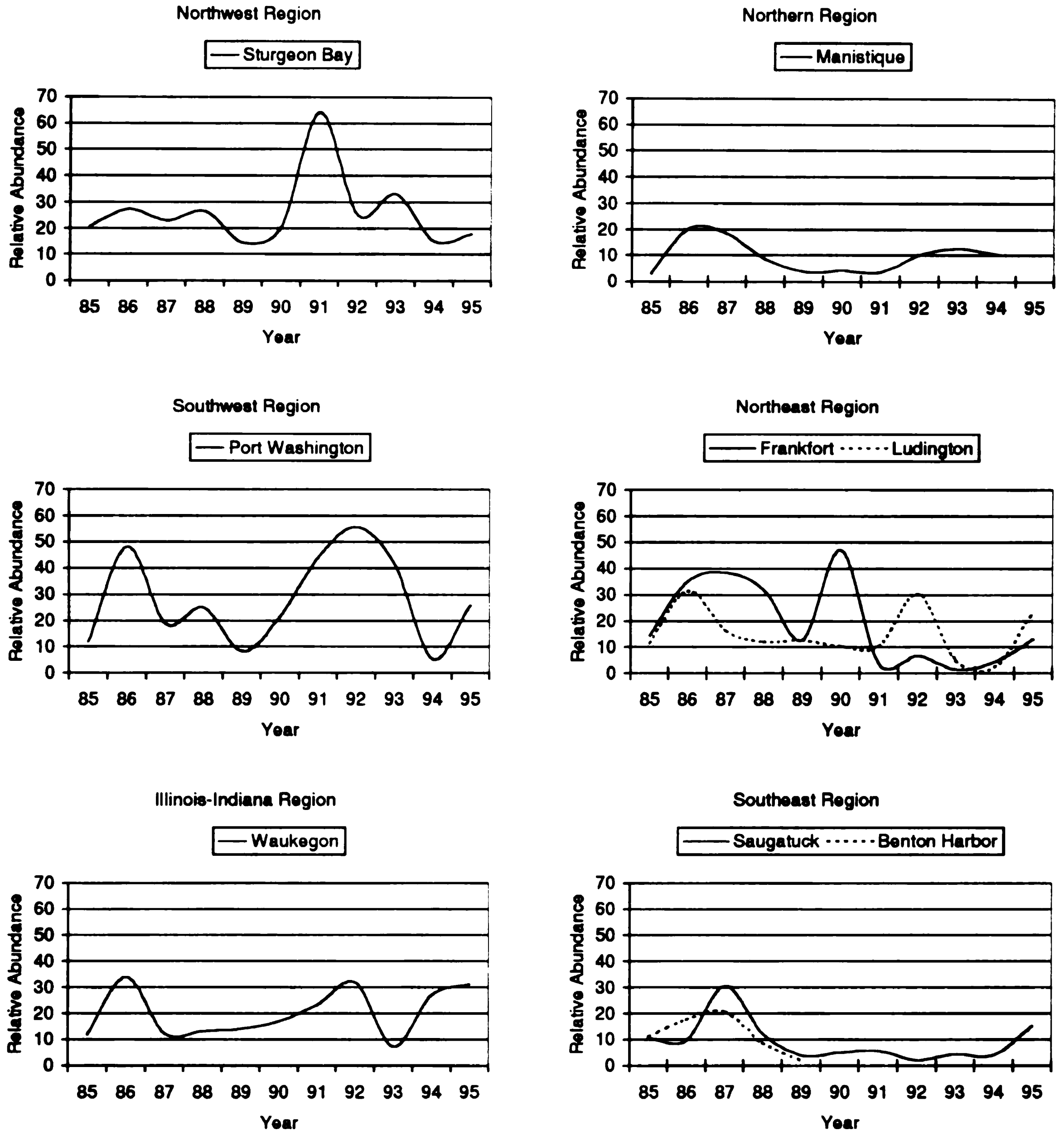

Figure 11. Relative alewife abundance from various regions of Lake Michigan, 1985-1995. Data are from Great Lakes Science Center annual fall bottom trawl surveys. Estimates are based on fitting a general linear mixed model to these data, including year and depth effects as well as port and year*port interactions (Ann Krause, Michigan State University, unpublished results).

Conclusion

The collapse of a fishery is often caused by overfishing, but this was not the case with the Lake Michigan chinook salmon fishery from 1987 to 1992. The chinook salmon population is driven by annual stocking, and returns to the fishery declined despite the maintenance of high stocking levels. Chinook salmon suffered high mortality rates due in part to bacterial kidney disease, while the underlying cause of the disease is probably related to nutritional stress due to a decline in the abundance of alewives. Additional stress may be temperature-related, as most visual accounts of mortality occur in early spring, when water temperatures are coldest.

The decline of the fishery differed across regions. A complete collapse of the fishery was seen in the eastern regions of the lake, although declines in effort and harvest were observed in all regions. The greatest declines occurred in the Northeast and Southeast regions that traditionally had the highest levels of stocking, effort, harvest, and harvest rates. With a decline in the fishery came a change in the distribution of the harvest. For example, 21% of the lake-wide chinook salmon stocking in 1985 occurred in the Southeast region, and accounted for 25% of the lake-wide harvest of the 1985 year class. By 1992, stocking in that region increased to 27% of the lake-wide total, while year class harvest fell to 13% of the lake-wide total. In contrast, stocking in the Northwest region of the 1985 year class was 19% of the lakewide total, and year class harvest was 16%. By 1992, stocking in the Northwest region decreased to 9% of the lake-wide total, and year class harvest increased to 34% of the lake-wide total. The relative contributions of the Green Bay, North, and Illinois-Indiana regions to the lake-wide harvest remained relatively constant for the 1985 to 1992 year classes.

Trends in the sport fishery data suggest that a change in the spatial distribution of chinook salmon was the driving force behind regional differences in the decline of the fishery. Increases in lake-wide mortality probably contributed to these declines, but spatial differences in mortality are unlikely to be the primary cause of these differences. Tagging studies and similar harvest size distributions show that chinook salmon do not form distinct subpopulations, but rather mix widely. Most likely chinook salmon migrated in response to local stresses, and concentrated in the western regions of the lake when alewife abundance in the eastern regions declined.

CHAPTER THREE

LAKE-WIDE STOCK ASSESSMENT MODEL

Introduction

The Pacific salmon stocking program in Lake Michigan began in the late 1960s in response to the extirpation of native lake trout (*Salvelinus namaycush*) stocks and high abundance of exotic alewives (*Alosa pseudoharengus*) (Eshenroder et al. 1995). The immediate popularity of these introduced salmonine species to the sport fishery, as well as a growing fishery-related industry, prompted state agencies to maintain an intensive stocking program. Numbers of salmonines planted in Lake Michigan peaked in 1984 at 17 million fish (Holey 1995; Chapter 2). However, beginning in 1987 the thriving salmonine fishery of the mid-1980s underwent a substantial decline in angling success and harvest. This was largely due to a dramatic decline in the chinook salmon population despite the maintenance of consistent stocking levels (Bence and Smith in press; Chapter 2). While explanations for the decline have included the prevalence of a bacterial kidney disease, the root of the problem may be that current levels of stocking are too high, leading to a scarcity of forage fish, nutritional stress, and BKD-induced mortality (Stewart et al. 1981; Stewart and Ibarra 1991; Koonce and Jones 1994). Little is known, in the quantifiable sense, about the impact of BKD-related mortality on the population (Clark 1996).

The Michigan DNR Division of Fisheries has recently expressed the need for using more rigorous modeling analyses to develop lake-wide stocking plans for salmonines (Clark 1996). Similarly, the Lake Michigan Committee of the Great Lakes Fishery Commission has called for more mathematical modeling of existing data to help establish detailed management plans, and species-specific harvest levels for salmonines in Lake Michigan (Eshenroder et al. 1995). Ultimately, decisions on what species to stock, how many to stock, and where to stock them could be crucial toward reviving the chinook salmon fishery in Lake Michigan.

I have approached this problem using a population model based on catch-at-age-analysis (CAA) (Megrey 1989). This study is unique to salmonine dynamics of Lake Michigan because it incorporates an integrated modeling and data analysis approach not previously used for Lake Michigan salmonines (Sitar 1996).

The goal of this study was to quantify the contributions of three sources of mortality, (1) fishing mortality, (2) spawning mortality, and (3) time-varying natural mortality, to the total annual mortality of chinook salmon from 1985-1996. Furthermore, model parameters and estimates of age-specific abundance can be used as improved inputs in tropho-dynamic models for Lake Michigan (e.g. SIMPLE, Koonce and Jones 1994).

The Michigan DNR (MDNR) is currently addressing this issue with a multi-species model, CONNECT, which is designed to predict ideal stocking levels required to meet fish community objectives for salmonines in Lake Michigan (Rutherford 1997). While novel in its approach, the current CONNECT model for chinook salmon was not rigorously fit to all available data using an optimization routine, as would be done in a

CAA model. Other recent modeling work on chinook salmon in the Great Lakes involves a CAA model built for chinook in Lake Huron (Bence and Meehan unpublished). The Lake Michigan chinook model presented here builds on the information used by CONNECT and the structure of the Lake Huron CAA model.

Methods

The stock assessment model is an age-structured, deterministic model that estimates abundance for multiple cohorts. Initial cohort abundance is assumed to be known, and the model accounts for changes in abundance due to various sources of mortality.

Population Model

The basic idea of the population model is that population abundance at the start of a given year is equal to the abundance at the start of the previous year, multiplied by the proportion of that population that survives the year. Survival is a function of a continuous-time instantaneous mortality rate, such that:

$$N_{y+1} = N_y e^{-Z_y} \qquad (1)$$

Lake Michigan chinook salmon population dynamics do not follow equation 1 because not all sources of mortality function in a continuous fashion over a yearly period. Preliminary analysis of sport harvest data indicates that most of the in-lake fishing mortality occurs in July and August. Similarly, analysis of weir return data suggests that most of the spawning-related mortality occurs in September and October. Chinook salmon population dynamics in Lake Michigan can be more accurately modeled using an approach that combines both continuous-time and discrete-time sources of mortality (Kope 1987; Bence and Meehan unpublished).

Abundance

Chinook salmon abundance for a cohort at the start of a calendar year was assumed to be a function of abundance of the cohort at the start of the previous year, natural mortality, fishing mortality, and maturation mortality, such that:

$$N_{a+1,y+1} = N_{a,y} e^{-M_{a,y}} (1 - P_{F_{a,y}})(1 - P_{MAT_a}) \tag{2}$$

where $M_{a,y}$ is an instantaneous natural mortality rate (for age-a and year-y), $P_{Fa,y}$ is the annual proportion of the population removed by the fishery, and P_{MATa} is the annual proportion of the population that matures and returns to the streams to spawn and die.

Natural Mortality

Natural mortality ($M_{a,y}$) is an instantaneous annual rate and is assumed to operate independently of fishing mortality (Hilborn and Walters 1992). Most CAA models assume a constant natural mortality rate that applies to all ages (Megrey 1989), however, we know that the natural mortality rate for chinook salmon in Lake Michigan increased in the late 1980's in response to an outbreak of bacterial kidney disease (Johnson and Hnath 1991). In order to quantify the changes in natural mortality during the study period, I modeled mortality as a sum of a constant component, and a time-varying (TVM) component, such that the total natural mortality rate ($M_{a,y}$) is:

$$M_{a,y} = M_a + M_{TVM_{a,y}} \tag{3}$$

Age-specific natural mortality (M_a) was assumed to be a known constant, estimated prior to the onset of BKD-related mortality (Table 14). I derived an estimate of the age-0 mortality rate based upon previous modeling work on Lake Michigan salmonines during pre-BKD mortality years (Stewart et al. 1981). Mortality rate estimates for ages 1-3 were based upon estimates from west-coast populations (Rutherford 1997). I assumed that mortality rates for ages 4-5 were equal to age-3 mortality, because any increase in mortality rates for older fish would be accounted for by TVM and maturation mortality.

Age- and year-specific TVM was estimated by the model. I assumed that TVM affected age groups in a logistic fashion, with ages 0-5 being increasingly affected. This assumption reflected observations of BKD mortality (Nelson and Hnath 1990), and approximated assumptions of BKD mortality rates from CONNECT (Rutherford 1997) The logistic mortality function was:

$$M_{TVM\,a,y} = \frac{\gamma_y}{1+e^{-\alpha(a-\beta)}} \tag{4}$$

where a is age, γ_y is a year-specific TVM intensity parameter, and α and β are parameters that determine the shape of the logistic function. The model estimated $\ln(\gamma_y)$, $\ln(\alpha)$, and $\ln(\beta)$ as formal parameters. This logistic model forced a relationship between age-specific rates within years, while the year-specific TVM intensity parameters were unrelated between years. BKD mortality did not appear to be a significant source of mortality in Lake Michigan chinook until about 1987 (Clark 1996). Since that time, BKD-infected chinook have been observed in the population at varying levels of incidence (Clark 1996). I allowed the model to estimate TVM from 1985 to 1996. Initial parameter values were chosen that matched age- and year-specific TVM with age- and year-specific estimates of BKD mortality rates reported in the CONNECT model (Rutherford 1997).

Fishing Mortality

Fishing mortality is assumed to be an instantaneous event, occurring at the end of July. I felt that this fishery more closely represents a seasonal, or pulse, fishery as opposed to a continuous fishery. An identical approach was used for Lake Huron chinook (Bence and Meehan unpublished). The proportion of the population removed by the fishery ($P_{F_{a,y}}$) was estimated as:

$$P_{F_{a,y}} = 1 - e^{-F_{a,y}} \tag{5}$$

where $F_{a,y}$ is an instantaneous mortality rate per unit time that occurs over an infinitesimally short time unit. $F_{a,y}$ operates under a separability assumption (Megrey 1989) and is a function of age-specific fishery selectivity (S_a) and year-specific fishing intensity (f_y), such that:

$$F_{a,y} = S_a f_y \tag{6}$$

Selectivity to the sport fishery was assumed constant over time. Selectivity was also assumed to operate in a logistic fashion where ages 0-5 were increasingly selected for by the fishery, such that:

$$S_a = \frac{1}{1 + e^{-\alpha(a-\beta)}} \tag{7}$$

where α and β determined the shape of the logistic curve, and $\ln(\alpha)$ and $\ln(\beta)$ were formal parameters estimated by the model. A maximum selectivity value of 1 indicated that an age group was fully selected to the fishery.

Year-specific fishing intensities (f_y) were estimated by the model, with $\ln(f_y)$ estimated as formal parameters from 1985 through 1995. For 1967 to 1984, fishing int

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intensity was assumed to increase linearly from zero to the 1985 level estimated by the model (Jones et al. 1993).

Maturation (Spawning) Mortality

Similar to fishing mortality, maturation mortality (MAT) was assumed to be an instantaneous event, occurring immediately after fishing mortality and before additional natural mortality. Age-specific maturation was assumed to increase in a logistic fashion from age 0 to age 4, while MAT for age-5 was assumed to equal 1. The maturation function for ages 0 through 4 was:

$$P_{MAT_a} = \frac{1}{1 + e^{-\alpha(a-\beta)}} \tag{8}$$

where $\ln(\alpha)$ and $\ln(\beta)$ were estimated as formal parameters. I assumed all chinook salmon reached maturity by age-5 because few age-6 fish are observed in the fishery and fishery-independent surveys.

Catch

Sport fishery catch, or harvest, was assumed to occur as an instantaneous event, during which time the population was subject to no other sources of mortality, and after 7 months of natural mortality had taken place (Bence and Meehan unpublished). A common approach in catch-at-age analysis is to assume that fishing mortality operates in an approximately continuous fashion, thereby warranting the use of the standard Baranov equation to estimate catch (Hilborn and Walters 1992). For intensely seasonal fisheries, the approach taken here can provide a better approximation of catch than the Baranov equation (Mertz and Myers 1996). Catch is the proportion of the population abundance remaining after seven months that dies from fishing, and is estimated by:

$$C_{a,y} = N_{a,y} e^{-M_{a,y} 7/12} P_{F_{a,y}} \tag{9}$$

To better estimate age-specific maturation, I estimated the age composition of mature chinook salmon harvested by the fishery. Mature chinook harvested by the fishery is the proportion of the harvest that has reached maturity, and is estimated by:

$$C_{MAT_{a,y}} = C_{a,y} P_{MAT_a} \tag{10}$$

Effort

Sport fishery effort is related to year-specific fishing intensity divided by an assumed constant catchability coefficient (q), such that:

$$E_y = \frac{f_y}{q} \tag{11}$$

where $\ln(q)$ is a formal parameter estimated by the model.

Observed Data and Other Model Inputs

Recruitment

Chinook salmon are stocked in the spring as age-0 fingerlings. Lake-wide stocking data from 1967 to 1996 was collected from the Departments of Natural Resources from Wisconsin, Illinois, Indiana, and Michigan (Chapter 2). In the modern era, no chinook were stocked in Lake Michigan prior to 1967. Recruitment to age-0 of naturally reproduced chinook has been steadily increasing over time (Clark 1996). Input data for natural recruitment were taken from Rutherford (1997), and are based on estimates of natural reproduction from Carl (1980; 1982; and 1984), Seelbach (1985 and 1986), Zafft (1992), and Hesse (1994). Age-0 recruitment is the sum of stocked fingerlings and estimated wild smolts. Recruitment is an input into the model and is not used as observed data to the fit the model. The model assumes that recruitment to age-0 occurs at the beginning of the year.

Sport Fishery Information

Harvest and effort information was compiled from data collected by creel survey programs run by each of the four states surrounding the lake (Chapter 2). I attempted to use effort that was directly targeting chinook salmon, although I had to compromise due to differences in creel survey programs. For Wisconsin data, effort was estimated from interviews in which anglers specifically indicated they were targeting chinook salmon. For Illinois and Indiana, I used effort targeted at all salmonine species. I estimated Michigan effort from raw creel data using interviews in which anglers indicated they were targeting chinook salmon, coho salmon, salmon in general, or salmon and trout in general. Targeted effort used for this model differs from targeted effort reported in Chapter 2, which was defined as effort that was targeting all salmonines. The model uses harvest and effort data to estimate changes in population abundance. I used chinook salmon effort in the model to avoid any bias due to possible changes in effort not directed at chinook salmon. Post hoc comparison, however, of chinook harvest rates calculated from chinook salmon effort versus salmonine effort showed the same trends. Chinook salmon total harvest estimated from total angling effort (including non-targeted effort) was used for each state.

Michigan is the only one of the four states that collects substantial harvest age composition data. Wisconsin collects length composition data. Preliminary analysis of length compositions between Michigan and Wisconsin indicate similar harvest length compositions. Therefore, I assumed that age composition of the lake-wide harvest could be reasonably estimated by the age composition of the Michigan harvest. Chinook salmon migrate widely within Lake Michigan and even between Lake Michigan and Lake Huron (Clark 1996), suggesting that stocks are reasonably mixed, and therefore that the age composition of the population may be fairly homogenous.

Michigan also collects data on maturity of chinook salmon sampled from the fishery. From these data, the age composition of mature fish harvested by the fishery was estimated. These age compositions of mature chinook were based on sampling data from July 15 to August 31. This time period was chosen so that maturation was advanced enough that identification of maturity would not be difficult, though not so advanced that aging error due to scale erosion would be a problem. Model estimates of mature age composition were fit to empirical estimates in order to provide additional information on maturation schedules of chinook.

Weir Harvest Information

Harvest data from Michigan and Wisconsin weirs are available from 1985 to the present. Prior to 1985, only Michigan collected weir information. I generated an estimate of the lake-wide weir harvest age composition for 1985 to 1996, weighted by the number of chinook sampled from each of the weirs around the lake. Questions about the validity of sampled age compositions, coupled with the inconsistencies of reported age compositions between years, prevented the use of weir harvest information in the model prior to 1985.

Fitting the Model to Observed Data

Model estimates of effort, total harvest and mature harvest, harvest and mature harvest age compositions, and weir harvest age compositions were fit to observed data from 1985 to 1996. Model parameters were iteratively and independently adjusted in order to provide the best fit. Fit was measured with a log-likelihood function, and best fit was reached when the log-likelihood function was maximized (Methot 1990). A quasi-Newton search algorithm was used to find the maximum likelihood, with forward differencing used to estimate the partial derivatives of the objective function. Parameters were estimated using quadratic extrapolation. The log-likelihood equation was:

$$L = L_1 + L_2 + L_3 + L_4 + L_5 \tag{12}$$

where L_1 was the log-likelihood of the model fit to observed fishery effort data, L_2 was the log-likelihood of the model fit to observed fishery harvest, L_3 was the log-likelihood of the model fit to observed fishery harvest age composition, L_4 was the log-likelihood of the model fit to observed fishery mature harvest age composition, and L_5 was the log-likelihood of the model fit to observed weir harvest age composition. No external weighting was applied to any of the likelihood functions (see Methot 1990). Errors were assumed to be log-normally distributed for L_1 and L_2 such that the log-likelihood functions were defined as:

$$L_{1,2} = -0.5 \sum_y \frac{\ln(\lambda_y^{obs}) - \ln(\lambda_y^{pred})}{\sigma_y^2} \tag{13}$$

where λ_y^{obs} and λ_y^{pred} are the observed and predicted effort and harvest. The standard deviation (σ) was set at 0.06 for effort and 0.08 for harvest, and was estimated as:

$$\sigma = \sqrt{\ln[(CV)^2 + 1]} \tag{14}$$

Law and Kelton (1982). I estimated an average coefficient of variation (*CV*) from observed annual effort and harvest estimates from Michigan's waters of Lake Michigan (See Chapter 2).

Errors were assumed to be multinomially distributed for the age composition log-likelihood functions, such that they were defined (ignoring constants) as:

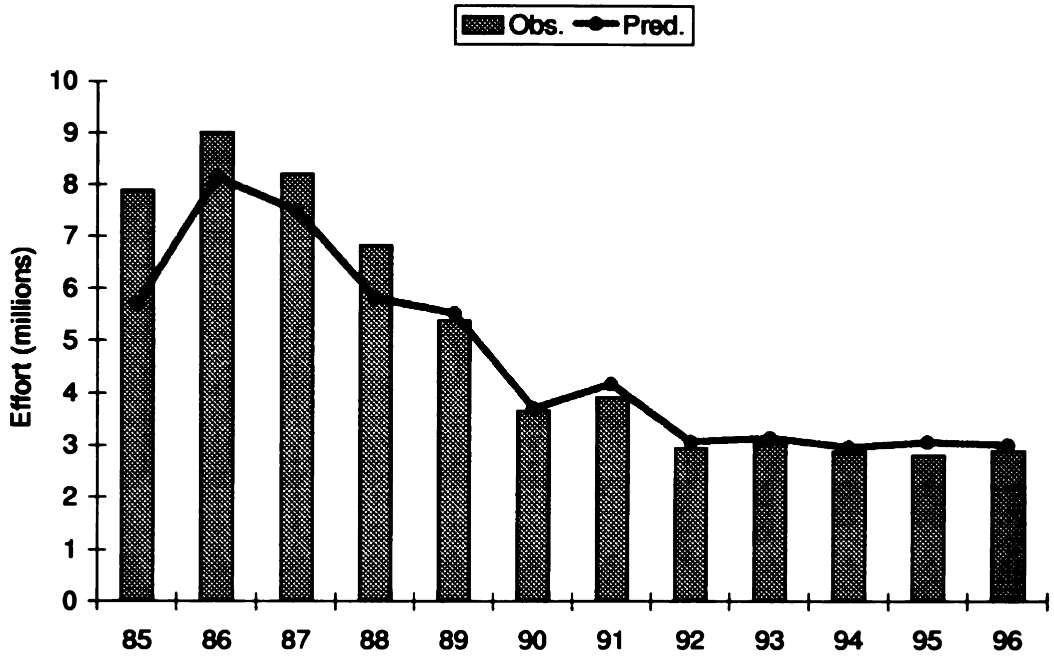
$$L_{3,4,5} = \sum_{y} n_{y} \sum p_{a,y}^{obs} \ln(p_{a,y}^{pred}) \qquad (15)$$

where n_y is the effective sample size in year y, and $p_{a,y}^{obs}$ and $p_{a,y}^{pred}$ are the observed and predicted proportions at age *a* in year *y*. The effective sample size in the likelihood functions for the harvest, mature harvest, and weir harvest age compositions was set to 100, 50, and 50 respectively. These values represent subjective judgements about the accuracy of the observed data. (For a discussion of this issue see Fournier and Archibald (1982)). I have more confidence in the observed harvest age composition than the mature harvest and the weir harvest age compositions because of aging error caused by (1) scale erosion or (2) problems associated with the use of an age-length key to estimate weir harvest age compositions.

Results

Fishery Effort and Harvest

The model fit the observed fishery effort and harvest data reasonably well, but had more difficulty fitting 1985-1988 data versus 1989-1996 data (Figure 12). Chinook salmon effort and harvest increased from 1985 to 1986 before declining through 1994. Effort was relatively constant from 1994 to 1996, while harvest increased. The model was generally able to follow these declines. There was an obvious tradeoff as the model attempted to fit fishery effort and avoid overestimating harvest for 1985-88. The result was an underestimation of the decline in effort and an overestimation of the decline in harvest. A pattern in effort and harvest residuals shows that effort and harvest errors are correlated, which is to be expected because both are related to the fishing intensity parameter, f_y (Figure 13).



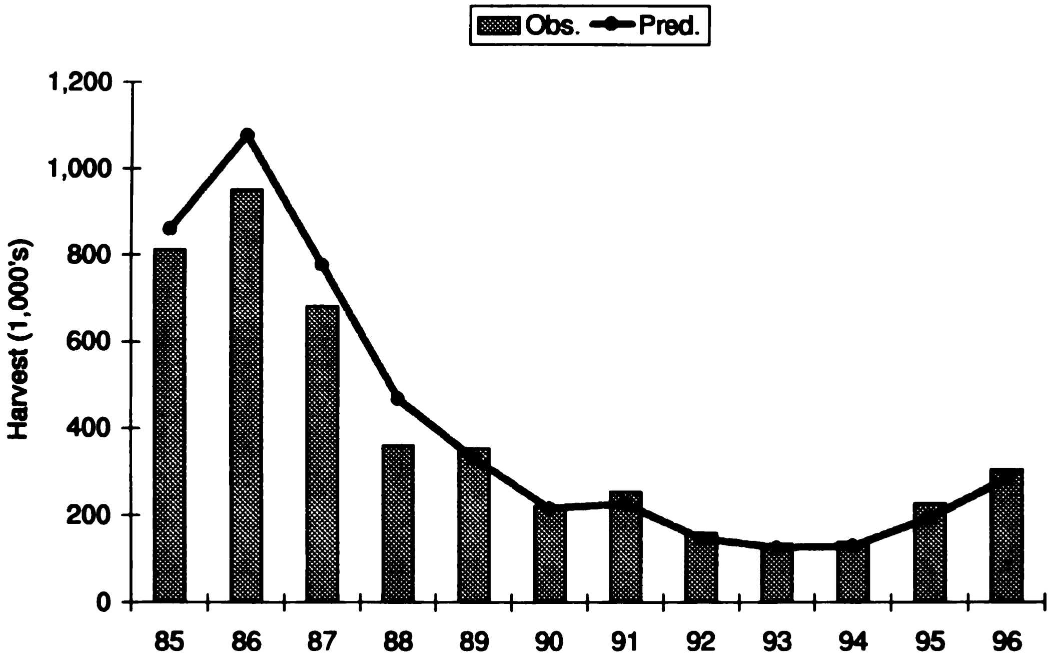


Figure 12. Observed and predicted values of sport fishery effort in millions of angler-hours (top) and chinook salmon harvest in thousands of fish (bottom).

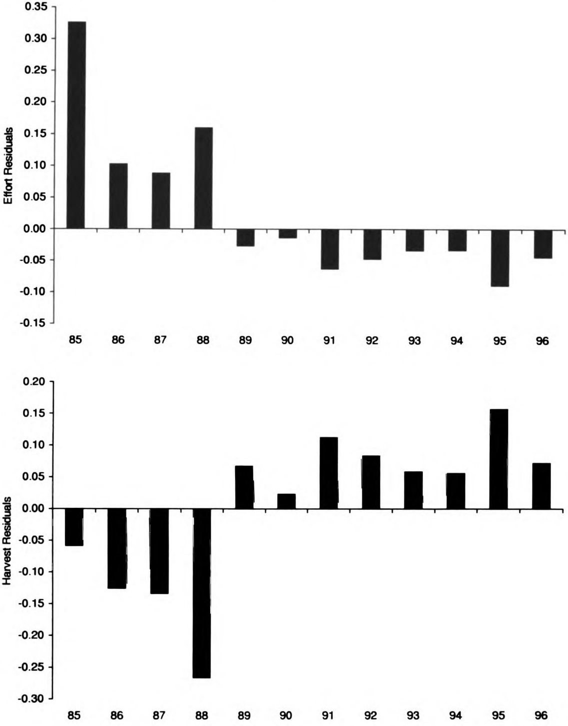


Figure 13. Log$_e$-based residuals from model predictions of fishery effort (top) and chinook salmon harvest (bottom) for the Lake Michigan sport fishery.

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Age Compositions

The onset of additional natural mortality in the late 1980's resulted in a decline of older age classes from the population, and this decline was reflected in the fishery and weir age composition data. Fishery harvest consisted primarily of 2 and 3-year old fish from 1985 to 1989, with more 3 and 4-year old fish harvested than 1 and 2-year old fish in most years (Table 20). From 1990 to 1995, the harvest age composition shifted to consist primarily of 1 and 2-year old fish, with 1-year old fish dominating the harvest in some years, and with more 1-year old fish harvested than 3-year old fish in all years.

Similar trends were seen in the age composition of mature fish harvested by the fishery and in the weirs. Age 3-4 fish dominated the mature harvest from 1985 to 1989 (Table 21). In 1990, the age composition shifted to mostly age 2-3 fish along with an equal proportion of age-1 and age-4 fish. Weir harvest age compositions were comprised of age 2-4 fish from 1985 to 1990, but shifted to age 1-3 fish from 1991 to 1996 (Table 22).

I examined patterns in standardized residuals to evaluate model fit to observed age composition data. Standardized residuals were estimated as:

$$SR = \frac{p_{a.y}^{obs} - p_{a.y}^{pred}}{\sqrt{p_{a.y}^{pred}(1 - p_{a.y}^{pred})/n_{eff}}} \qquad (16)$$

where $p_{a.y}$ is the proportion at age a in year y from the observed and predicted age composition data, and n_{eff} is the effective sample size.

The model had difficulty fitting the fishery age composition data, as evidenced by clear patterns in the standardized residuals (Figure 14). The proportion of age-0 fish in the harvest was consistently overestimated, while the proportion of age-1 fish was consistently underestimated. The model also consistently overestimated the proportion of age-2 fish. Residuals are more randomly distributed and the magnitude of the residuals decreases for ages 3-5. These patterns are probably a result of the difficulty the model has when estimating the true selectivity with a logistic function. The logistic function cannot follow the slope of the true selectivity function, so it compromises by overestimating age-0, underestimating age-1, and overestimating age-2. One solution would be to allow the model to estimate age-specific selectivity without the constraint of a forcing function. An immediate solution would be to set age-0 selectivity to zero, since very few age-0 fish are observed in the fishery harvest.

Similar patterns in the standardized residuals are also evident in the weir harvest age composition data. Most notable is the model's tendency to overestimate age-0 and underestimate age-1 fish, and was likely due to the inability of the logistic function to follow the true maturation rates. Residual patterns for age 2-4 fish show a definite transition between 1990 and 1991, and reflect the model's inability to follow the abrupt change in the observed age composition data (Figure 15).

Abrupt changes in age composition data are also reflected in the standardized residuals for the fishery mature harvest age compositions. Most notable is the increase in the residuals for age-1 fish from 1989 to 1990, as the model cannot follow the rapid increase in age-1 harvest from 1990 to 1993 (Figure 16). Residuals appear to be randomly distributed for ages 2-4. The model consistently overestimates the proportion of age-0 and age-5 fish, although differences from observed data are small.

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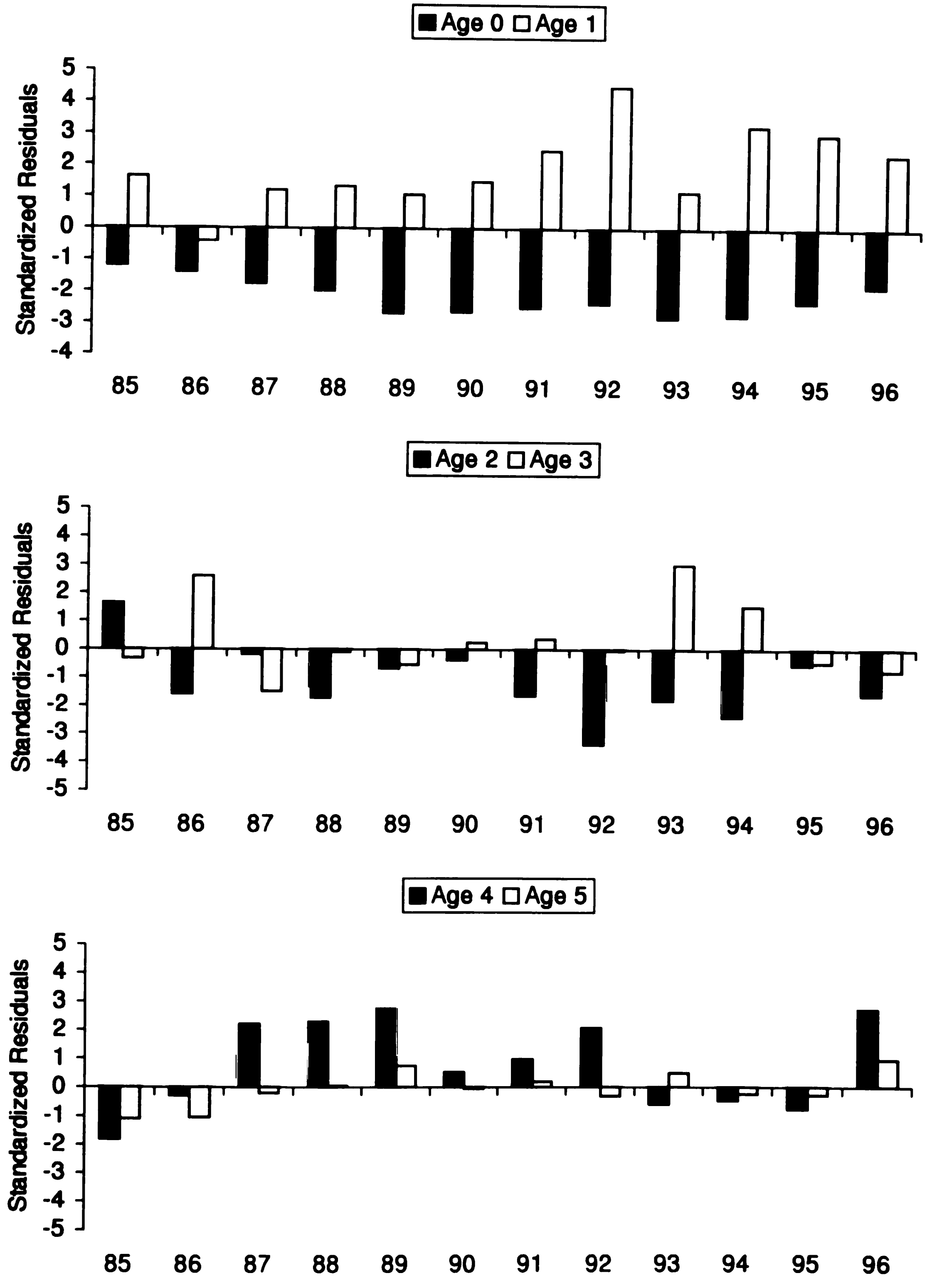

Figure 14. Standardized residuals for fishery harvest age compositions of chinook salmon in Lake Michigan. See text for calculation of standardized residuals.

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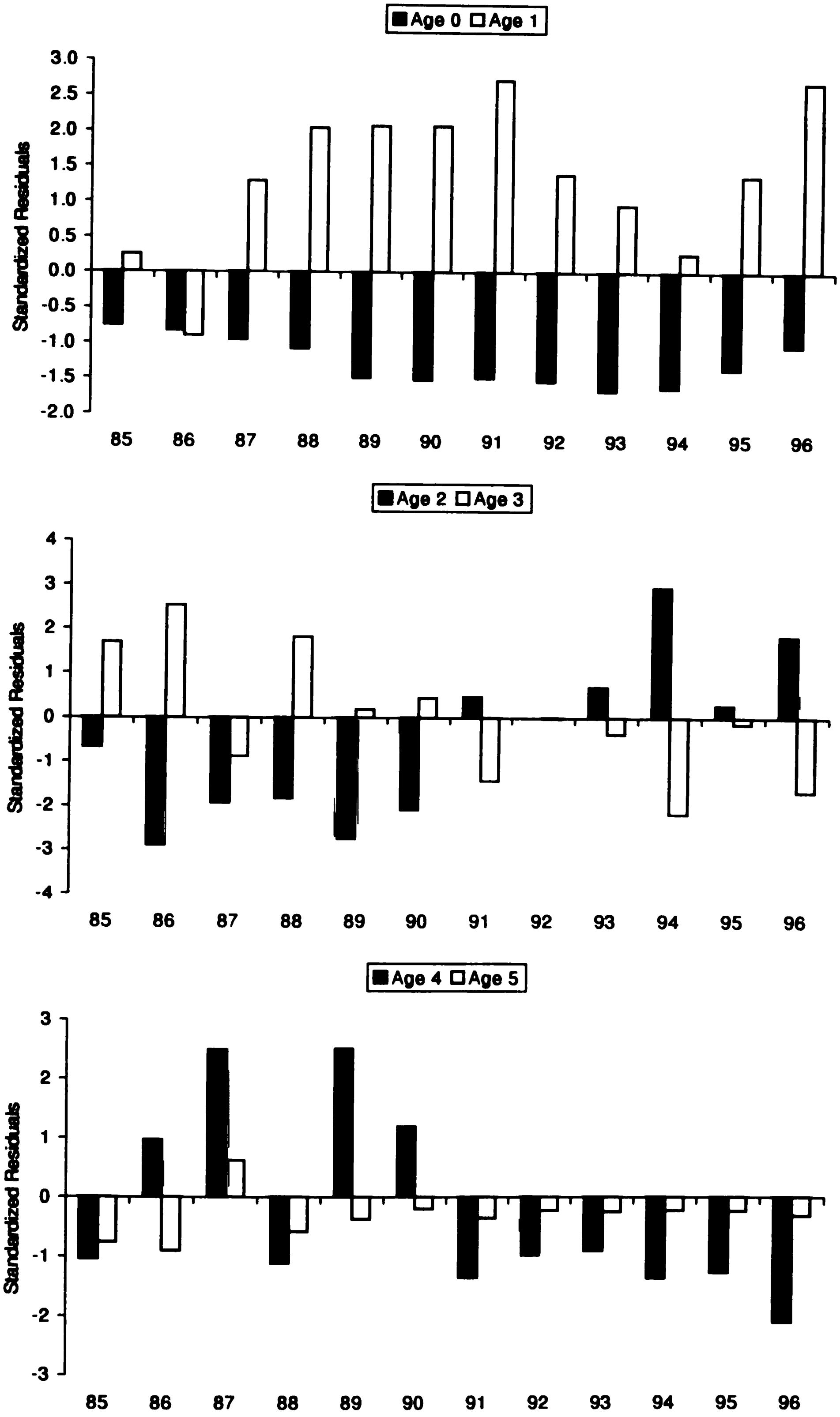

Figure 15. Standardized residuals for weir harvest age compositions of chinook salmon from Lake Michigan. See text for calculation of standardized residuals.

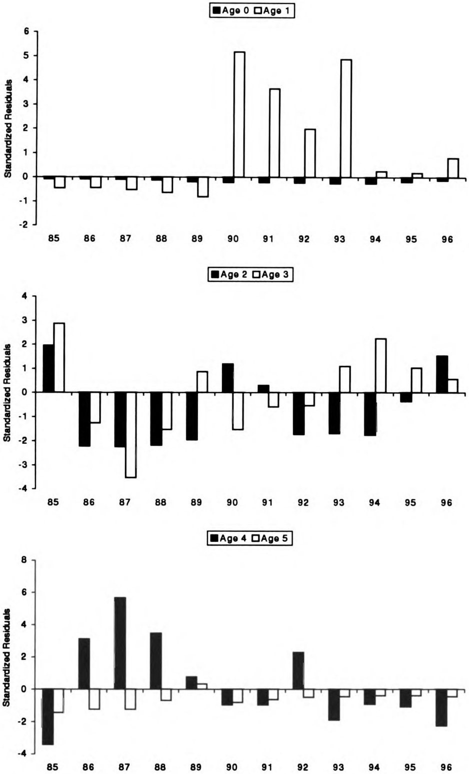

Figure 16. Standardized residuals for fishery mature harvest age compositions of chinook salmon in Lake Michigan. See text for calculation of standardized residuals.

Fishing Mortality

Fishing mortality is estimated by the model for ages 0-5 from 1967 to 1996. Fishing mortality has had relatively little impact on age 0 and age 1 chinook salmon, with mortality never exceeding 3% in any year for either age class (Table 13). Thus although the model did not accurately estimate harvest of the younger ages (0, 1), these errors had only minor influence on the predicted dynamics. Age-2 fishing mortality reached a peak of 13% in 1986, and declined to 5% by 1992. Ages 3-5 chinook suffer peak fishing mortality levels in 1986, from 30% and 41%, and declined to 13-18% by 1992.

Maturation

Model-estimated proportions of chinook salmon that matured for ages 0-4 were 0.00, 0.02, 0.13, 0.51, and 0.87. Age-5 maturity was set to 1 (Table 19). Note that these proportions do not indicate the proportion that return to the streams, since some mature fish are harvested by the fishery. Total harvest of mature fish from weirs and from the fishery were not fit to observed data because observed weir harvest data does not account for all chinook that run up all streams tributary to Lake Michigan. Therefore, only the age compositions of the fishery mature harvest and weir harvest are used to compare with observed data (Table 21; Table 22).

Natural Mortality

I established baseline age-specific natural mortality rates that I assumed to operate over the entire study period. These rates were set at 0.75 and 0.30 for ages 0 and 1, respectively, and 0.10 for ages 2 to 5 (See **Methods**). Mortality rates were held constant for older ages because I assumed that any additional mortality for older fish would be accounted for by TVM and maturation.

BKD-related deaths of chinook salmon were not observed in Lake Michigan until 1986, but I allowed the model to estimate TVM beginning in 1985. The model estimated a TVM rate of 0.00 for ages 0 and 1, and estimated that the same TVM rate applied for ages 2 to 5. TVM increased for ages 2 to 5 from 0.00 in 1985 to a peak of 1.70 in 1993 before declining to 0.29 in 1996 (Table 18).

There is some concern that the logistic model applied to TVM may have been too restrictive. In particular, the fact that the model estimates equal values for ages 2 to 5 may suggest that TVM for older ages, if given the freedom, might actually decline. I did not test this by fitting a different curve to the model, but I did test the baseline CAA model against a model that estimated TVM separately for each age and year. I compared the baseline CAA model against the new model using a likelihood ratio test (Seber and Wild 1989). Allowing the model to independently estimate TVM for each age and year significantly improved model fit ($P<0.005$). TVM estimates for ages 0 and 1 continued to be relatively small, but estimates for ages 2 to 5 were markedly different across ages, with no consistent trends across ages or years. If there is time-varying mortality among ages, I would expect it to have some systematic pattern so that in a given year close ages would respond the same way. Instead, mortality rates varied without pattern. This may not reflect time-varying mortality but rather an over-parameterization of this alternative model, which uses these new parameters to explain other process errors such as differential catchability or aging errors.

Total Mortality

The model does not allow survival past age 5, therefore total annual mortality of age 5 is 100%. Age 0 and age 1 chinook are not exposed to TVM mortality and very little fishing mortality, that total annual mortality of these ages has remained relatively steady from 1967 to 1995, at 53% and 28% for age 0 and age-1, respectively (Table 15). Estimated TVM appears to have the greatest effect on ages 2 and 3. Pre-TVM mortality averaged 25% and 61% for ages 2 and 3, respectively. Total annual mortality increased substantially for these age groups during TVM years, averaging 66% and 83% for ages 2 and 3, respectively. Annual mortality before 1985 for age 4 chinook salmon averaged 91%, and increased to 96% after 1985. Highest total annual mortality for all ages was observed from 1991 to 1994, which corresponds with the lowest harvest years, though not the highest fishing mortality years.

A comparison of total number of deaths in each year from 1985 to 1996 indicates that relative contributions of different sources of mortality shifted over time after 1985. For age-3 fish, for example, natural mortality accounted for 12% of the total deaths, but increased to 54% after 1985. Fishing mortality accounted for 20% prior to 1985 and declined to 15% after 1985. Spawning mortality comprised 68% of the total annual mortality for age-3 fish prior to 1985, but declined to 31% after 1985 as natural mortality increased. It is clear that the increase in natural mortality caused a decline in maturation deaths and harvest, as most BKD infected fish were not surviving to reach the weirs or to be caught by anglers.

Population Abundance

Assuming that fishing intensity (f_y) increases linearly from 1967 to 1985, I used the model to estimate abundance from 1967 to 1996 (Table 16). Chinook salmon were first stocked into Lake Michigan in 1967; therefore, age-5 fish do not appear in the population until 1972. Total recruitment reached a peak in 1989 at 10 million chinook salmon. Recruitment fluctuated between 7.5 million and 10 million from 1986 to 1996, and was driven by stocking and steady increases in estimated natural reproduction. The model estimated that the population size was less than 1 million in 1967, and surpassed 10 million by 1978. Population size fluctuated between 13.5 million and 17.9 million from 1980 to 1996, with a peak abundance in 1990.

Standing stock biomass was estimated from the model's estimate of abundance-at-age and the estimated mean weight at annulus formation from the CONNECT model (Rutherford 1997). Stock biomass increased from 1967 to a peak level of 50 million pounds in 1986 before high mortality rates on older chinook salmon caused the biomass to decline beginning in 1987 (Figure 17; Table 17). Stock biomass declined by nearly 50% from 1986 to 26 million pounds by 1993. Natural mortality rates have been declining in 1995 and 1996, and stock biomass has increased to 39 million pounds in 1996.

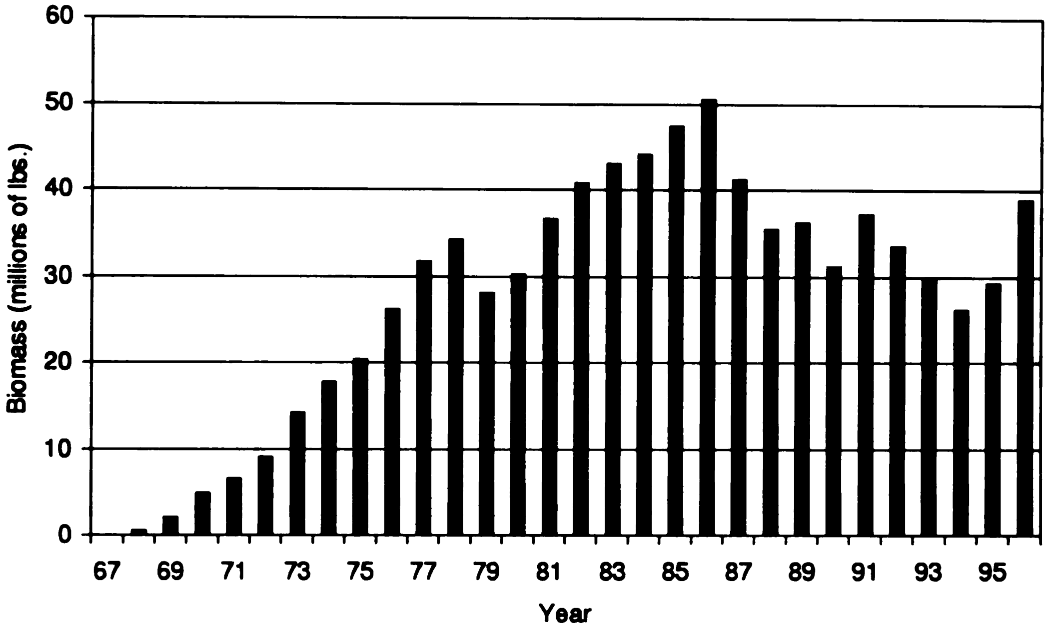

Figure 17. Standing stock biomass (pounds) as estimated from abundance-at-age from the CAA model, and mean weight at annulus formation from CONNECT (Rutherford 1997).

Uncertainty of Parameter Estimates

I estimated 95% confidence intervals for each parameter by inverting the likelihood ratio test (Seber and Wild 1989) (Table 18). Uncertainty for the time-varying mortality parameter (TVM_y) was variable across years, with the largest uncertainty associated with the 1985 and 1996 parameters. High variability for the 1996 parameter was probably due to the lack of information on mortality in 1997. Estimating uncertainty about the parameters determining the shape of the mortality function proved difficult. Nevertheless, the model showed a strong tendency to set age 0-1 mortality to zero and make age 2-5 mortality equivalent, although this could be accomplished with various combinations of α and β. The lower 95% confidence limit on the logistic function parameter α resulted in zero TVM for age 0 and a small level of time-varying natural mortality for age 1 chinook salmon, with essentially equal (and higher) TVM for ages 2-5. The upper 95% confidence limit went to infinity as mortality of ages 0-1 went to zero and mortality of ages 2-5 was constant (i.e. a step function). Confidence limits on the logistic function parameter β could not be estimated because the model would increase α until the denominator in the TVM function (Equation 4) approached zero, causing the model to crash. I found this to be a limitation with Microsoft Excel©, because preliminary model runs in Gauss™ did not crash.

Discussion

Severe declines in the Lake Michigan chinook salmon fishery in the late 1980's prompted fishery managers to evaluate chinook salmon management efforts in an attempt to revive the fishery (Clark 1996). Declines in the chinook salmon fishery were likely due to density-dependent mortality, as evidenced by an outbreak of BKD and declines in fishery catch rates, and were probably caused by nutritional stress due to declines in the alewife population.

This model is a first attempt to quantify relationships between different sources of mortality on chinook salmon during a period of critical and substantial changes in chinook population dynamics. In order to use this model to make predictions or projections for the future, I would need to add to the model additional assumptions about how these population dynamics will operate in the future. One assumption would be that these rates would remain constant at their current (1996) values, but my analysis of the past suggests that this is probably not correct (Chapter 2). Accurate forecasts would need to account for how vital rates change in response to chinook salmon abundance and other factors, and this would require an improved mechanistic understanding. However, mortality and abundance estimates made by the model can be used to improve existing Lake Michigan multi-species models (e.g. Rutherford 1997; Stewart et al. 1981; Jones et al. 1993).

I conducted a sensitivity analysis of the age-0 baseline natural mortality rate (0.75). Age-0 was increased and decreased by 25% and the model was re-fit to the data for both trials. Model output from both trials was compared to the original results to see if adjusting the natural mortality rate would result in the same qualitative conclusions of chinook salmon population dynamics. Both trials in fact yielded the same qualitative results as the original model (Table 18; Table 23; Table 24). However, a 25% reduction in age-0 natural mortality appeared to significantly improve model fit, and raised concerns about the appropriate estimate of natural mortality. Because empirical evidence (declines in observed weir returns per fish stocked; Chapter 2) points to an increase in age-0 mortality in the mid-1980s, simply decreasing the input of natural mortality in order to improve model fit does not seem justified.

The results of this model suggest that chinook salmon suffered very high mortality in the late 1980s and early 1990s, with most of the mortality due to increasing natural mortality. Ages 2 through 5 were subject to equivalent TVM rates within years, and all four age groups suffered severe declines in abundance over a year. Consequently, the mode in the age composition of the harvest shifted from age 3 to age 2.

Initial values for time-varying mortality were obtained from existing estimates of BKD mortality rates (Rutherford 1997). However, because the model does not fit any observed data on BKD mortality, inferences about BKD mortality based on model-estimated time-varying mortality should be made carefully. In particular, the model estimated an annual increase in TVM from 1985 to 1993, followed by a decline from 1993 to 1996 (Figure 18). In contrast, observed data show greater levels of BKD incidence in the late 1980's, followed by declines in the early 1990's (Marcquenski 1997; Clark 1996). This discrepancy between the model estimates of mortality and observed incidence rates of BKD could mean one of two things. First, observed incidence rates of BKD are not an index of BKD mortality rates (Clark 1996). Second, causes of mortality rates may be more complex than originally thought, and cannot be estimated by simply observing one of the symptoms (i.e., BKD incidence).

High in-lake natural mortality rates on age 2-5 chinook are a real problem in Lake Michigan, and the reduction of natural mortality, similar to reduction of sea lamprey mortality, should be an immediate management goal. If mortality is density dependent (Clark 1996), then reducing the population density of chinook salmon is a viable method for reducing mortality and improving the fishery. Because chinook salmon recruitment is governed by stocking in Lake Michigan, management decisions regarding stocking will influence population abundance.

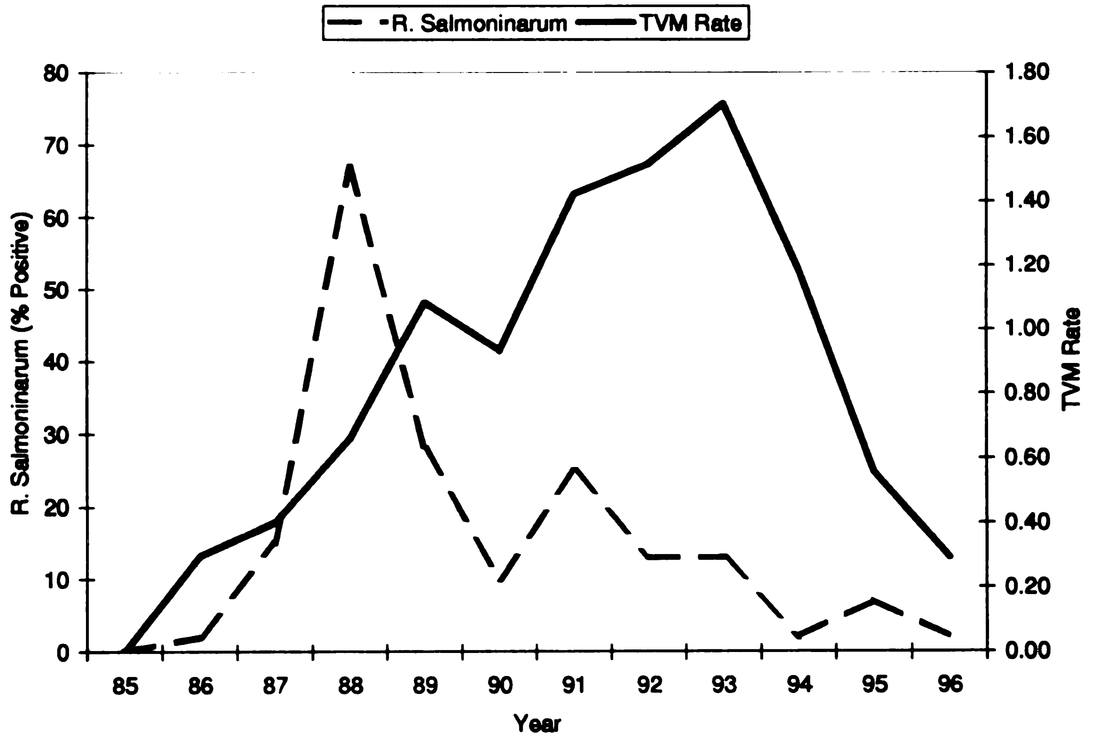

Figure 18. Observed estimates of prevalence of *Renibacterium salmoninarum*, the causative of agent of BKD, versus model-estimated time-varying instantaneous natural mortality rate (TVM). Observed data was obtained from mature chinook salmon sampled at Strawberry Creek, Sturgeon Bay, Wisconsin (Marcquenski 1997).

CHAPTER FOUR

CONCLUSIONS

The chinook salmon population in Lake Michigan underwent dramatic changes between 1986 and 1996. These changes were most directly felt by the sport fishery, as harvest and harvest rates for chinook salmon began declining in 1987, triggering a decline in sport fishery effort, which led to a cycle of further declines in harvest. Greatest declines in the fishery were seen in the Michigan waters of the lake along the eastern shoreline, where chinook salmon harvest declined by 95%. Complete collapse of the entire salmonine sport fishery, however, was avoided. The fishery that was once dominated by chinook salmon harvest was able to diversify and maintain high harvest rates by targeting other salmonine species. Part of the reason for spatial differences in trends in the chinook salmon fishery was due to changes in the spatial distribution of chinook salmon, as evidenced by spatial differences in harvest rate trends. It is likely that chinook salmon concentrated in the western regions of the lake in response to spatial changes in the distribution of alewives, their primary forage.

The sport fishery was not the only place where changes in the chinook salmon population were felt. Dead chinook salmon washed up on the southern Lake Michigan shoreline in the late 1980's, suggesting an increase in lake-wide natural mortality. While most of these fish ultimately died from BKD, it is likely that another environmental or nutritional stress affected their resistance to disease. Regardless of the cause, modeling results show that this increase in lake-wide natural mortality was a significant source of mortality in older (age 2-5) chinook salmon, accounting for upwards of 70% of the deaths in some years. The increased mortality of older chinook salmon could not be explained by overfishing, which is often to blame for fishery collapses. Because of increased natural mortality of older fish, fishery harvest declined, and fishery and weir harvest age compositions shifted towards younger ages, as fewer older fish survived to be harvested. Finally, estimated standing stock biomass declined by about 50% from peak levels in the mid-1980's, to the early-1990's. The population appears to be recovering in recent years as harvest and harvest rates are increasing, and age compositions are slowly shifting towards older fish. Preliminary analysis of 1997 fishery data show further increases.

While the initial objective of this study was to build a spatial model of chinook salmon population dynamics in Lake Michigan, I soon realized that there was much more work to be done compiling the necessary data than was previously thought. A spatial analysis of trends in the chinook salmon fishery grew out of the need to re-estimate the time series of harvest and effort from the Michigan sport fishery, and showed that there were distinct spatial differences in fishery trends that may be explained by chinook movements. Coded wire tagging studies support this possibility, and both studies could be combined to further understand chinook salmon movements. More important, theories about movements could lay the groundwork towards a spatial model. A spatial model of chinook salmon population dynamics could estimate spatial differences in mortality rates and abundance, and would be useful in determining different stocking scenarios.

What is the future of chinook salmon in Lake Michigan? It seems that as the fishery grew in the 1970's and 1980's, chinook salmon became an indispensable species in the fish community. Because chinook salmon were originally stocked in part to control alewives, it is ironic to think that as the chinook fishery collapsed, the commercial fishery for alewives was reduced. It seems that the success of the salmonine fishery in Lake Michigan has dictated fishery management goals. Fish community objectives, as outlined by the Great Lakes Fishery Commission (Eshenroder et al. 1995), have called for a diverse salmonine fish community capable of sustaining an annual yield of 6 to 15 million pounds. Included is a short-term goal of annual yields of chinook salmon of about 6.8 million pounds. Also included is the goal of an increased reliance upon naturally reproduced salmonines. With what appears to be a recovery in the chinook salmon population in recent years, their popularity in the fishery, and their ability to naturally reproduce, chinook salmon will continue to be an integral part of the Lake Michigan fish community.

Management of chinook salmon in the next 10 years will continue to be challenged by a number of issues, and several unanswered questions remain. For example, chinook salmon health continues to be monitored by measuring BKD incidence rates in surveys and in the weirs, although it is not clear what the relationship is between incidence rates and mortality rates. Reducing stocking rates could alleviate mortality rates (Clark 1996; Keller et al. 1990), but exactly how many fish should be stocked and in what species combinations is an area for further research. The answer is complicated by uncertainty surrounding estimates of forage abundance.

APPENDIX:

ADDITIONAL TABLES

Table 1. Number of salmonine fingerlings stocked in Lake Michigan, by species, 1963 to 1996.

	Species						
Year	Brook trout	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout	Total
1963	0	0	0	0	0	0	0
1964	0	0	0	0	0	0	0
1965	0	0	0	0	0	0	0
1966	20,000	16,300	0	0	0	81,299	117,599
1967	0	12,540	802,390	0	569,600	74,695	1,459,225
1968	0	172,400	686,692	0	0	0	859,092
1969	0	57,200	717,585	0	0	22,200	796,985
1970	0	94,540	1,903,492	0	0	362,088	2,360,120
1971	0	531,804	2,215,198	0	208,000	702,579	3,657,581
1972	9,980	722,740	2,032,128	0	405,400	465,832	3,636,080
1973	0	1,313,842	3,045,767	313,700	300,000	1,532,270	6,505,579
1974	4,000	469,300	3,578,053	0	260,250	1,261,815	5,573,418
1975	0	82,647	4,275,782	156,200	149,000	894,061	5,557,690
1976	61,290	387,922	3,302,057	352,728	0	392,669	4,496,666
1977	524,772	362,200	2,818,561	0	47,500	143,661	3,896,694
1978	30,000	854,247	5,365,263	0	65,000	1,284,753	7,599,263
1979	0	663,947	5,184,271	511,506	120,271	1,667,085	8,147,080
1980	2,560	753,074	6,105,924	244,486	268,700	1,620,094	8,994,838
1981	89,070	578,440	4,747,799	101,953	560,500	847,700	6,925,462
1982	193,477	1,516,793	6,146,427	245,581	707,347	1,410,712	10,220,337
1983	210,035	1,578,114	6,291,913	127,555	31,480	1,709,163	9,948,260
1984	85,481	1,149,178	7,709,792	439,704	445,920	1,755,442	11,585,517
1985	130,739	1,127,110	5,955,523	139,018	1,158,423	631,128	9,141,941
1986	25,460	719,318	5,692,678	246,352	822,600	629,729	8,136,137
1987	53,277	811,485	5,800,757	299,429	24,984	378,371	7,368,303
1988	135,050	783,652	5,416,870	939,153	623,600	371,960	8,270,285
1989	6,000	753,140	7,859,479	608,324	3,371,122	536,978	13,135,043
1990	208,700	936,747	7,128,723	1,206,152	0	418,722	9,899,044
1991	203,000	639,296	6,237,562	815,515	0	654,428	8,549,801
1992	109,700	765,382	5,795,465	1,225,339	673,621	385,399	8,954,906
1993	142,300	869,905	5,529,950	130,105	0	417,558	7,089,818
1994	119,400	1,244,853	5,892,950	710,082	1,357,821	874,559	10,199,665
1995	271,932	1,014,458	6,590,976	1,030,639	0	287,990	9,195,995
1996	105,330	816,765	6,193,377	1,021,630	143,629	345,336	8,626,067

Table 2. Number of salmonine yearlings stocked in Lake Michigan, by species, 1963 to 1996.

	Species					
Year	Brook trout	Brown trout	Coho salmon	Lake trout	Rainbow trout	Total
1963	0	0	0	0	9,200	9,200
1964	0	0	0	0	15,000	15,000
1965	0	0	0	1,273,878	24,830	1,298,708
1966	29,240	21,700	659,356	1,766,190	194,290	2,670,776
1967	32,809	35,935	1,732,298	1,854,820	40,230	3,696,092
1968	49,481	79,190	1,183,872	1,875,900	389,349	3,577,792
1969	33,518	84,377	3,237,856	1,999,805	409,454	5,765,010
1970	49,500	129,820	3,535,930	1,960,000	294,189	5,969,439
1971	93,048	177,311	2,743,046	2,135,545	665,849	5,814,799
1972	94,782	203,469	2,619,908	2,520,120	850,220	6,288,499
1973	50,150	598,953	2,265,257	2,209,150	1,546,452	6,669,962
1974	30,250	363,358	3,230,972	2,137,100	905,888	6,667,568
1975	61,300	425,345	2,368,691	2,428,424	734,928	6,018,688
1976	25,820	653,188	2,843,671	2,547,800	1,473,445	7,543,924
1977	98,480	793,525	3,088,218	2,370,100	1,058,108	7,408,431
1978	218,225	655,202	2,658,941	2,474,400	651,767	6,658,535
1979	192,970	548,202	3,832,337	2,376,601	865,394	7,815,504
1980	205,000	554,564	2,698,884	2,522,600	1,040,119	7,021,167
1981	119,397	591,242	2,349,478	2,081,530	1,094,020	6,235,667
1982	51,226	642,821	1,934,960	2,038,790	1,116,517	5,784,314
1983	87,403	670,682	2,236,817	2,209,590	1,016,864	6,221,356
1984	147,561	653,768	2,514,343	1,119,140	1,360,818	5,795,630
1985	185,226	670,437	2,519,665	2,623,399	1,193,695	7,192,422
1986	171,436	714,735	2,045,045	2,474,406	1,671,942	7,077,564
1987	79,000	529,684	2,005,142	1,973,350	1,447,628	6,034,804
1988	361,936	761,627	2,243,742	1,922,628	1,058,959	6,348,892
1989	144,100	750,835	1,725,601	2,005,600	1,308,187	5,934,323
1990	191,448	841,024	1,173,901	1,317,115	1,181,337	4,704,825
1991	123,100	743,983	1,655,396	2,779,482	1,320,495	6,622,456
1992	162,720	849,225	1,516,871	2,761,244	1,437,414	6,727,474
1993	151,794	888,817	1,578,646	2,697,835	1,422,809	6,739,901
1994	149,185	927,527	761,291	2,545,512	1,376,435	5,759,950
1995	56,025	861,602	1,367,189	2,264,428	1,762,601	6,311,845
1996	69,464	969,981	2,075,803	1,971,448	1,499,149	6,585,845

Table 3. Total number of salmonines stocked in Lake Michigan, by species, from 1986-1996. Includes fingerlings, yearlings, and lake trout fry.

	Species						
Year	Brook trout	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout	Total
1963	0	0	0	0	0	9,200	9,200
1964	0	0	0	0	0	15,000	15,000
1965	0	0	0	0	1,273,878	24,830	1,298,708
1966	49,240	38,000	0	659,356	1,766,190	275,589	2,788,375
1967	32,809	48,475	802,390	1,732,298	2,424,420	114,925	5,155,317
1968	49,481	251,590	686,692	1,183,872	1,875,900	389,349	4,436,884
1969	33,518	141,577	717,585	3,237,856	1,999,805	431,654	6,561,995
1970	49,500	224,360	1,903,492	3,535,930	1,960,000	656,277	8,329,559
1971	93,048	709,115	2,215,198	2,743,046	2,343,545	1,368,428	9,472,380
1972	104,762	926,209	2,032,128	2,619,908	2,925,520	1,316,052	9,924,579
1973	50,150	1,912,795	3,045,767	2,578,957	2,509,150	3,078,722	13,175,541
1974	34,250	832,658	3,578,053	3,230,972	2,397,350	2,167,703	12,240,986
1975	61,300	507,992	4,275,782	2,524,891	2,577,424	1,628,989	11,576,378
1976	87,110	1,041,110	3,302,057	3,196,399	2,547,800	1,866,114	12,040,590
1977	623,252	1,155,725	2,818,561	3,088,218	2,417,600	1,201,769	11,305,125
1978	248,225	1,509,449	5,365,263	2,658,941	2,539,400	1,936,520	14,257,798
1979	192,970	1,212,149	5,184,271	4,343,843	2,496,872	2,532,479	15,962,584
1980	207,560	1,307,638	6,105,924	2,943,370	2,791,300	2,660,213	16,016,005
1981	208,467	1,169,682	4,747,799	2,451,431	3,142,030	1,941,720	13,661,129
1982	244,703	2,159,614	6,146,427	2,180,541	3,176,137	2,527,229	16,434,651
1983	297,438	2,248,796	6,291,913	2,364,372	2,541,070	2,726,027	16,469,616
1984	233,042	1,802,946	7,709,792	2,954,047	2,195,060	3,116,260	18,011,147
1985	315,965	1,797,547	5,955,523	2,658,683	5,081,822	1,824,823	17,634,363
1986	196,896	1,434,053	5,692,678	2,291,397	4,197,006	2,301,671	16,113,701
1987	132,277	1,341,169	5,800,757	2,304,571	3,298,334	1,825,999	14,703,107
1988	496,986	1,545,279	5,416,870	3,182,895	2,546,228	1,430,919	14,619,177
1989	150,100	1,503,975	7,859,479	2,333,925	5,376,722	1,845,165	19,069,366
1990	400,148	1,777,771	7,128,723	2,380,053	1,317,115	1,600,059	14,603,869
1991	326,100	1,383,279	6,237,562	2,470,911	2,779,482	1,974,923	15,172,257
1992	272,420	1,614,607	5,795,465	2,742,210	3,434,865	1,822,813	15,682,380
1993	294,094	1,758,722	5,529,950	1,708,751	2,697,835	1,840,367	13,829,719
1994	268,585	2,172,380	5,892,950	1,471,373	3,903,333	2,250,994	15,959,615
1995	327,957	1,876,060	6,590,976	2,397,828	2,264,428	2,050,591	15,507,840
1996	174,794	1,786,746	6,193,377	3,097,433	2,115,077	1,844,485	15,211,912

Table 4. Number of chinook salmon fingerlings stocked in Lake Michigan, by region, from 1967 to 1996.

Year	Region							Total
	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	
1967	0	0	591,830	0	210,560	0	0	802,390
1968	0	0	321,912	0	364,780	0	0	686,692
1969	0	0	300,000	66,000	351,585	0	0	717,585
1970	100,000	200,034	408,900	119,000	965,558	0	110,000	1,903,492
1971	100,934	0	557,248	254,000	1,105,412	10,000	187,604	2,215,198
1972	124,528	0	597,290	180,000	993,634	113,000	23,676	2,032,128
1973	442,750	102,700	608,406	340,000	1,181,390	197,000	173,521	3,045,767
1974	140,496	201,578	854,282	356,400	889,596	220,000	915,701	3,578,053
1975	519,321	353,947	911,215	400,600	1,187,284	366,275	537,140	4,275,782
1976	454,340	202,880	588,229	692,000	903,109	281,500	179,999	3,302,057
1977	397,340	25,095	525,528	245,000	804,921	332,608	488,069	2,818,561
1978	554,000	100,000	1,018,362	862,000	1,305,192	701,149	824,560	5,365,263
1979	395,000	50,000	1,053,098	863,200	1,203,602	905,611	713,760	5,184,271
1980	684,200	150,156	1,250,846	797,300	1,451,890	998,000	773,532	6,105,924
1981	618,800	50,000	979,231	557,100	1,125,516	723,160	693,992	4,747,799
1982	434,479	100,094	1,101,573	970,300	1,423,940	1,009,700	1,106,341	6,146,427
1983	554,900	365,495	1,187,250	1,283,200	1,318,085	811,000	771,983	6,291,913
1984	587,850	550,108	1,231,109	1,255,000	1,973,063	1,169,000	943,662	7,709,792
1985	595,756	481,912	857,095	1,125,000	1,239,020	1,107,000	549,740	5,955,523
1986	555,000	600,080	845,164	1,020,000	1,213,141	902,567	556,726	5,692,678
1987	460,000	594,700	823,787	1,000,000	1,168,939	903,484	849,847	5,800,757
1988	326,000	684,390	986,543	728,150	1,277,528	455,143	959,116	5,416,870
1989	622,624	816,697	1,122,792	1,156,711	1,849,089	1,110,580	1,180,986	7,859,479
1990	514,000	719,059	1,204,768	870,722	1,745,519	1,118,609	956,046	7,128,723
1991	382,600	675,956	1,039,962	680,613	1,628,604	787,405	1,042,422	6,237,562
1992	387,176	683,534	1,215,067	495,859	1,589,615	741,092	683,122	5,795,465
1993	349,740	614,030	1,061,780	539,951	1,506,709	801,079	656,661	5,529,950
1994	348,780	697,833	1,128,613	577,907	1,767,838	718,370	653,609	5,892,950
1995	365,874	749,606	1,202,145	625,532	1,935,320	794,780	917,719	6,590,976
1996	394,260	680,346	1,158,390	623,768	1,580,688	818,929	936,996	6,193,377

Table 5. Lake Michigan total sport fishery effort and targeted salmonine effort, total salmonine harvest, and salmonine targeted harvest rate from 1986 to 1996. Does not include stream fishery.

		Salmonines		
Year	Total Effort	Targeted Effort	Total Harvest	Targeted Harvest Rate
1986	14,171,232	8,639,616	1,827,816	0.163
1987	12,486,847	7,394,333	1,436,853	0.146
1988	12,446,497	6,728,453	1,068,753	0.118
1989	10,839,150	5,417,639	1,323,159	0.155
1990	8,857,896	3,941,503	855,166	0.152
1991	9,461,886	4,121,606	883,339	0.152
1992	7,902,011	3,209,131	746,374	0.159
1993	7,727,446	3,393,389	849,328	0.174
1994	7,267,320	3,230,568	865,479	0.181
1995	7,108,768	3,191,348	826,370	0.176
1996	6,501,426	3,185,371	878,181	0.191

Table 6. Salmonine harvest by the Lake Michigan sport fishery, 1986 to 1996. Does not include the stream fishery.

	Species						
Year	Brook trout	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout	Total
1986	3,565	170,959	948,915	324,622	311,774	67,980	1,827,816
1987	1,168	90,418	680,126	315,592	253,050	96,498	1,436,853
1988	4,452	72,702	357,325	265,374	266,668	102,232	1,068,753
1989	1,966	83,906	351,937	407,115	346,983	131,252	1,323,159
1990	4,444	70,928	220,399	239,215	221,268	98,912	855,166
1991	1,286	87,928	252,589	154,635	242,551	144,349	883,339
1992	3,104	62,844	158,097	247,887	136,723	137,719	746,374
1993	1,463	91,921	131,928	295,170	157,340	171,506	849,328
1994	6,303	109,366	136,921	292,072	154,050	166,767	865,479
1995	1,450	76,055	225,564	181,216	191,808	150,278	826,370
1996	364	67,898	303,893	249,569	114,911	141,546	878,181

Table 7. **Salmonine effort from the Lake Michigan sport fishery, by region, from 1986 to 1996. Does not include stream fishery.**

	Region							
Year	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	Total
1986	288,361	39,430	1,621,667	983,812	2,751,815	1,375,337	1,579,193	8,639,616
1987	231,145	245,187	1,398,749	933,803	1,837,411	1,412,317	1,335,721	7,394,333
1988	383,624	156,981	977,026	761,419	2,180,123	1,247,220	1,022,061	6,728,453
1989	369,962	166,959	902,139	494,276	1,748,471	753,816	982,017	5,417,639
1990	238,439	164,864	787,409	438,681	1,063,919	542,383	705,807	3,941,503
1991	204,915	193,587	722,407	432,870	1,385,944	479,729	702,155	4,121,606
1992	156,995	189,506	509,971	429,978	620,827	520,291	781,563	3,209,131
1993	149,826	168,422	793,741	444,376	648,165	431,771	757,089	3,393,389
1994	126,093	143,162	521,597	449,624	660,329	623,817	705,947	3,230,568
1995	155,511	144,039	423,690	444,093	711,150	617,728	695,138	3,191,348
1996	118,643	118,597	589,836	397,307	626,805	651,765	682,419	3,185,371

Table 8. Chinook salmon harvest by the Lake Michigan sport fishery, 1986 to 1996. Does not include stream fishery.

	Region							
Year	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	Total
1986	26,805	5,821	303,755	101,518	347,456	114,569	48,991	948,915
1987	26,053	23,246	222,315	113,248	129,168	127,509	38,588	680,126
1988	36,209	12,604	84,471	47,660	95,994	59,651	20,736	357,325
1989	41,577	6,905	55,819	82,574	86,927	59,095	19,040	351,937
1990	15,624	9,456	45,294	45,848	45,938	41,598	16,641	220,399
1991	20,581	7,183	54,623	56,622	38,403	49,654	25,523	252,589
1992	13,995	9,360	31,353	42,446	14,095	33,934	12,915	158,097
1993	5,633	3,904	27,189	45,699	16,323	24,021	9,159	131,928
1994	8,099	2,414	14,675	55,044	20,213	29,299	7,177	136,921
1995	21,498	3,976	27,894	59,516	24,288	76,104	12,288	225,564
1996	8,853	4,422	70,397	88,682	40,067	75,248	16,224	303,893

Table 9. Chinook salmon annual targeted harvest rates for the Lake Michigan sport fishery, 1986 to 1996. Does not include stream fishery.

	Region							
Year	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	Lake-wide
1986	0.062	0.075	0.127	0.071	0.117	0.060	0.031	0.087
1987	0.067	0.086	0.086	0.079	0.063	0.068	0.029	0.065
1988	0.076	0.059	0.063	0.036	0.034	0.034	0.020	0.039
1989	0.082	0.033	0.048	0.059	0.036	0.030	0.019	0.039
1990	0.046	0.039	0.051	0.047	0.040	0.031	0.024	0.039
1991	0.083	0.033	0.062	0.075	0.027	0.044	0.036	0.045
1992	0.047	0.044	0.042	0.049	0.021	0.023	0.017	0.030
1993	0.030	0.021	0.027	0.056	0.025	0.027	0.012	0.027
1994	0.024	0.016	0.024	0.071	0.030	0.020	0.010	0.028
1995	0.080	0.023	0.055	0.073	0.031	0.069	0.018	0.047
1996	0.030	0.036	0.090	0.110	0.063	0.066	0.024	0.064

Table 10. Estimated year-class harvest of chinook salmon for the Lake Michigan sport fishery. Does not include stream fishery.

	Region							
Year Class	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	Total
1985	30,145	13,239	129,702	71,869	115,144	78,293	26,037	464,431
1986	29,603	10,110	79,255	60,981	80,270	58,786	19,385	338,389
1987	24,297	6,871	45,121	49,610	56,635	41,685	14,988	239,206
1988	18,423	6,912	40,839	46,739	41,255	39,025	16,145	209,339
1989	14,476	7,189	38,602	41,963	29,738	36,301	16,270	184,539
1990	13,385	6,521	37,694	48,016	23,598	35,807	16,010	181,031
1991	10,256	6,087	26,743	47,200	16,577	30,740	10,613	148,216
1992	10,507	3,334	22,304	52,550	19,754	38,867	9,101	156,417

Table 11. Estimated year-class harvest ratio (harvest per number stocked) of chinook salmon for the Lake Michigan sport fishery. Does not include stream fishery.

	Region							
Year Class	Green Bay	North	Northeast	Northwest	Southeast	Southwest	Illinois-Indiana	Lake-wide
1985	5.1	2.7	15.1	6.4	9.3	7.1	4.7	7.8
1986	5.3	1.7	9.4	6.0	6.6	6.5	3.5	5.9
1987	5.3	1.2	5.5	5.0	4.8	4.6	1.8	4.1
1988	5.7	1.0	4.1	6.4	3.2	8.6	1.7	3.9
1989	2.3	0.9	3.4	3.6	1.6	3.3	1.4	2.3
1990	2.6	0.9	3.1	5.5	1.4	3.2	1.7	2.5
1991	2.7	0.9	2.6	6.9	1.0	3.9	1.0	2.4
1992	2.7	0.5	1.8	10.6	1.2	5.2	1.3	2.7

Table 12. Comparison of model predicted vs. observed targeted effort and total chinook salmon harvest. No lake-wide observed data are available prior to 1986.

	Effort		Harvest	
Year	Observed	Predicted	Observed	Predicted
1967		299,325		96
1968		598,649		835
1969		897,974		4,961
1970		1,197,299		16,804
1971		1,496,623		29,321
1972		1,795,948		47,133
1973		2,095,273		84,892
1974		2,394,597		123,256
1975		2,693,922		159,299
1976		2,993,247		220,913
1977		3,292,572		293,890
1978		3,591,896		348,764
1979		3,891,221		364,416
1980		4,190,546		411,812
1981		4,489,870		535,138
1982		4,789,195		638,076
1983		5,088,520		714,634
1984		5,387,844		767,788
1985	7,874,006	5,687,169	810,849	859,907
1986	9,006,345	8,128,072	948,915	1,076,211
1987	8,186,326	7,494,890	680,126	777,502
1988	6,820,940	5,813,923	357,325	466,441
1989	5,388,977	5,534,408	351,937	329,065
1990	3,661,795	3,710,544	220,399	215,425
1991	3,919,424	4,174,903	252,589	225,712
1992	2,929,243	3,070,331	158,097	145,432
1993	3,030,855	3,134,258	131,928	124,445
1994	2,868,956	2,966,548	136,921	129,493
1995	2,795,866	3,058,135	225,564	192,744
1996	2,881,261	3,010,768	303,893	282,749

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Table 13. Estimated annual fishing mortality ($P_{Fa,y}$).

			Age			
Year	0	1	2	3	4	5
1967	0.000					
1968	0.000	0.002				
1969	0.001	0.003	0.015			
1970	0.001	0.004	0.020	0.052		
1971	0.001	0.005	0.025	0.064	0.088	
1972	0.001	0.006	0.030	0.077	0.104	0.111
1973	0.001	0.007	0.034	0.089	0.121	0.128
1974	0.001	0.008	0.039	0.101	0.137	0.145
1975	0.002	0.009	0.044	0.113	0.153	0.162
1976	0.002	0.011	0.049	0.125	0.168	0.178
1977	0.002	0.012	0.054	0.136	0.183	0.194
1978	0.002	0.013	0.058	0.148	0.198	0.210
1979	0.002	0.014	0.063	0.159	0.213	0.225
1980	0.003	0.015	0.068	0.170	0.227	0.240
1981	0.003	0.016	0.072	0.181	0.241	0.255
1982	0.003	0.017	0.077	0.192	0.255	0.270
1983	0.003	0.018	0.082	0.202	0.268	0.284
1984	0.003	0.019	0.086	0.213	0.282	0.298
1985	0.004	0.020	0.091	0.223	0.295	0.311
1986	0.005	0.028	0.127	0.303	0.393	0.413
1987	0.005	0.026	0.118	0.283	0.369	0.388
1988	0.004	0.020	0.093	0.228	0.300	0.317
1989	0.003	0.019	0.088	0.218	0.288	0.305
1990	0.002	0.013	0.060	0.152	0.204	0.216
1991	0.003	0.015	0.067	0.169	0.226	0.240
1992	0.002	0.011	0.050	0.128	0.172	0.182
1993	0.002	0.011	0.051	0.130	0.175	0.186
1994	0.002	0.010	0.048	0.123	0.167	0.177
1995	0.002	0.011	0.050	0.127	0.171	0.182
1996	0.002	0.011	0.049	0.125	0.169	0.179

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Table 14. Estimated annual instantaneous natural mortality rates.

	Age					
Year	0	1	2	3	4	5
1967-85	0.750	0.300	0.100	0.100	0.100	0.100
1986	0.750	0.300	0.397	0.397	0.397	0.397
1987	0.750	0.300	0.503	0.503	0.503	0.503
1988	0.750	0.300	0.763	0.763	0.763	0.763
1989	0.750	0.300	1.182	1.182	1.182	1.182
1990	0.750	0.300	1.031	1.031	1.031	1.031
1991	0.750	0.300	1.523	1.523	1.523	1.523
1992	0.750	0.300	1.616	1.616	1.616	1.616
1993	0.750	0.300	1.801	1.801	1.801	1.801
1994	0.750	0.300	1.285	1.285	1.285	1.285
1995	0.750	0.300	0.658	0.658	0.658	0.658
1996	0.750	0.300	0.394	0.394	0.394	0.394

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Table 15. Estimated total annual mortality (A).

	Age					
Year	0	1	2	3	4	5
1967	0.529					
1968	0.529	0.277				
1969	0.529	0.278	0.227			
1970	0.530	0.279	0.230	0.578		
1971	0.530	0.279	0.234	0.583	0.897	
1972	0.530	0.280	0.238	0.589	0.899	1.000
1973	0.530	0.281	0.242	0.594	0.900	1.000
1974	0.530	0.282	0.246	0.600	0.902	1.000
1975	0.530	0.282	0.249	0.605	0.904	1.000
1976	0.530	0.283	0.253	0.610	0.906	1.000
1977	0.530	0.284	0.257	0.615	0.907	1.000
1978	0.530	0.285	0.261	0.620	0.909	1.000
1979	0.530	0.285	0.264	0.625	0.911	1.000
1980	0.530	0.286	0.268	0.630	0.912	1.000
1981	0.531	0.287	0.272	0.635	0.914	1.000
1982	0.531	0.288	0.275	0.640	0.916	1.000
1983	0.531	0.288	0.279	0.645	0.917	1.000
1984	0.531	0.289	0.283	0.650	0.919	1.000
1985	0.531	0.290	0.286	0.654	0.920	1.000
1986	0.532	0.296	0.491	0.769	0.949	1.000
1987	0.531	0.294	0.537	0.787	0.952	1.000
1988	0.531	0.290	0.633	0.823	0.959	1.000
1989	0.531	0.290	0.757	0.882	0.973	1.000
1990	0.530	0.285	0.709	0.851	0.964	1.000
1991	0.530	0.286	0.824	0.911	0.979	1.000
1992	0.530	0.283	0.836	0.915	0.979	1.000
1993	0.530	0.283	0.864	0.929	0.983	1.000
1994	0.530	0.283	0.772	0.881	0.971	1.000
1995	0.530	0.283	0.573	0.777	0.946	1.000

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Table 16. Model estimated abundance-at-age. Age-0 abundance is equivalent to recruitment.

	Age						
Year	0	1	2	3	4	5	Total
1967	802,390	0	0	0	0	0	802,390
1968	686,692	377,697	0	0	0	0	1,064,389
1969	717,585	323,177	273,070	0	0	0	1,313,831
1970	1,913,492	337,653	233,405	211,215	0	0	2,695,765
1971	2,265,198	900,210	243,602	179,632	89,179	0	3,677,822
1972	2,102,128	1,065,474	648,774	186,543	74,843	9,213	4,086,974
1973	3,245,767	988,588	767,065	494,330	76,695	7,591	5,580,037
1974	3,978,053	1,526,136	710,959	581,541	200,553	7,637	7,004,879
1975	4,875,782	1,870,105	1,096,384	536,312	232,818	19,606	8,631,006
1976	4,002,057	2,291,707	1,342,070	822,924	211,874	22,346	8,692,978
1977	3,618,561	1,880,692	1,642,890	1,002,297	320,807	19,965	8,485,212
1978	6,165,263	1,700,160	1,346,812	1,220,827	385,571	29,679	10,848,313
1979	5,984,271	2,896,177	1,216,240	995,811	463,432	35,021	11,590,952
1980	7,305,924	2,810,634	2,069,638	894,774	373,021	41,326	13,495,317
1981	6,247,799	3,430,740	2,006,382	1,515,002	330,745	32,658	13,563,325
1982	7,646,427	2,933,319	2,446,454	1,461,358	552,608	28,429	15,068,594
1983	7,791,913	3,589,304	2,089,529	1,772,982	525,998	46,634	15,816,360
1984	9,229,792	3,656,919	2,554,109	1,506,746	629,732	43,580	17,620,879
1985	7,475,523	4,330,946	2,599,468	1,832,548	528,099	51,224	16,817,808
1986	7,692,678	3,507,131	3,075,331	1,855,469	633,700	42,167	16,806,476
1987	7,800,757	3,603,561	2,468,933	1,565,936	427,794	32,366	15,899,346
1988	7,616,870	3,655,622	2,542,507	1,143,267	334,139	20,440	15,312,845
1989	10,059,479	3,573,163	2,594,625	933,360	202,614	13,644	17,376,885
1990	9,876,937	4,719,836	2,538,605	629,375	110,149	5,536	17,880,438
1991	8,643,262	4,639,423	3,374,990	738,005	93,629	3,913	17,493,222
1992	8,030,679	4,058,771	3,312,037	595,667	65,802	1,978	16,064,934
1993	7,729,950	3,773,688	2,908,863	542,438	50,815	1,355	15,007,109
1994	8,092,950	3,632,229	2,703,935	395,358	38,334	866	14,863,671
1995	8,790,976	3,803,194	2,604,125	617,832	47,190	1,106	15,864,424
1996	8,393,377	4,130,990	2,725,821	1,112,095	137,478	2,535	16,502,296

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Table 17. Standing stock biomass (pounds) as estimated from abundance-at-age from the CAA model, and mean weight at annulus formation from CONNECT (Rutherford 1997).

	Age					
Year	1	2	3	4	5	Total
1967	0	0	0	0	0	0
1968	453,237	0	0	0	0	453,237
1969	387,812	1,556,497	0	0	0	1,944,310
1970	405,184	1,330,407	3,062,616	0	0	4,798,206
1971	1,080,252	1,388,530	2,604,671	1,426,872	0	6,500,325
1972	1,278,569	3,698,010	2,704,880	1,197,483	176,351	9,055,293
1973	1,186,306	4,372,272	7,167,789	1,227,124	145,304	14,098,795
1974	1,831,363	4,052,469	8,432,350	3,208,851	146,188	17,671,220
1975	2,244,126	6,249,386	7,776,523	3,725,091	375,309	20,370,434
1976	2,750,049	7,649,801	11,932,392	3,389,984	427,752	26,149,977
1977	2,256,831	9,364,473	14,533,312	5,132,909	382,180	31,669,705
1978	2,040,192	7,676,829	17,701,993	6,169,140	568,132	34,156,287
1979	3,475,413	6,446,070	10,854,342	6,580,737	630,376	27,986,937
1980	3,372,761	10,969,081	9,753,040	5,296,894	743,869	30,135,646
1981	4,116,888	10,633,823	16,513,517	4,696,580	587,839	36,548,647
1982	3,519,982	12,966,204	15,928,801	7,847,028	511,723	40,773,738
1983	4,307,165	11,074,504	19,325,505	7,469,176	839,409	43,015,758
1984	4,388,303	13,536,777	16,423,534	8,942,200	784,434	44,075,248
1985	5,197,135	13,777,181	19,974,778	7,499,012	922,027	47,370,133
1986	4,208,557	16,299,253	20,224,616	8,998,544	759,010	50,489,981
1987	4,324,273	13,085,343	17,068,700	6,074,676	582,585	41,135,577
1988	4,386,746	13,475,286	12,461,609	4,744,777	367,921	35,436,339
1989	4,287,796	14,789,362	13,533,716	3,241,821	261,182	36,113,877
1990	5,663,803	14,470,050	9,125,936	1,762,384	105,964	31,128,137
1991	5,567,307	19,237,444	10,701,077	1,498,058	74,902	37,078,789
1992	4,870,525	18,878,611	8,637,176	1,052,834	37,860	33,477,005
1993	4,528,426	16,580,517	7,865,353	813,045	25,940	29,813,281
1994	4,358,675	15,412,428	5,732,688	613,344	16,577	26,133,711
1995	4,563,833	14,843,515	8,958,561	755,037	21,181	29,142,127
1996	4,957,188	15,537,178	16,125,380	2,199,645	48,533	38,867,924

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Table 18. Parameters and 95% confidence intervals as estimated by the model. See Methods for a discussion of confidence interval estimates.

Parameter	Symbol	Lower 95%	Estimate	Upper 95%
TVM	γ_{1985}	0.000	0.000	0.052
	γ_{1986}	0.086	0.297	0.507
	γ_{1987}	0.192	0.403	0.615
	γ_{1988}	0.426	0.663	0.904
	γ_{1989}	0.833	1.082	1.336
	γ_{1990}	0.675	0.931	1.193
	γ_{1991}	1.163	1.423	1.689
	γ_{1992}	1.255	1.516	1.782
	γ_{1993}	1.440	1.701	1.969
	γ_{1994}	0.941	1.185	1.433
	γ_{1995}	0.277	0.558	0.838
	γ_{1996}	0.000	0.294	0.747
	α	7.859	45.014	∞
	β	*	1.281	*
Fishing Intensity	f_{1985}	0.288	0.378	0.511
	f_{1986}	0.418	0.541	0.710
	f_{1987}	0.381	0.499	0.661
	f_{1988}	0.295	0.387	0.514
	f_{1989}	0.281	0.368	0.490
	f_{1990}	0.188	0.247	0.329
	f_{1991}	0.211	0.278	0.371
	f_{1992}	0.155	0.204	0.273
	f_{1993}	0.158	0.209	0.279
	f_{1994}	0.150	0.197	0.264
	f_{1995}	0.154	0.203	0.273
	f_{1996}	0.151	0.200	0.269
Selectivity	α	1.646	1.789	1.942
	β	2.385	2.609	2.863
Maturation	α	1.805	1.913	2.024
	β	2.898	2.984	3.072
Catchability Coefficient	q	5.142E-08	6.653E-08	8.747E-08

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Table 19. Estimated maturation and fishery selectivity. Values were estimated by logistic functions, with parameters estimated by the CAA model.

	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
Maturation (MAT_a)	0.00	0.02	0.13	0.51	0.87	1.00
Selectivity (S_a)	0.01	0.05	0.25	0.67	0.92	0.99

Table 20. Observed and predicted fishery harvest age compositions.

Observed Fishery Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.00	0.13	0.33	0.43	0.10	0.00
1986	0.00	0.07	0.22	0.54	0.17	0.00
1987	0.00	0.14	0.27	0.35	0.23	0.01
1988	0.00	0.18	0.24	0.35	0.22	0.01
1989	0.00	0.22	0.32	0.29	0.17	0.01
1990	0.00	0.30	0.37	0.25	0.07	0.00
1991	0.00	0.36	0.33	0.24	0.06	0.00
1992	0.01	0.45	0.28	0.20	0.07	0.00
1993	0.00	0.33	0.33	0.32	0.02	0.00
1994	0.00	0.39	0.36	0.24	0.02	0.00
1995	0.00	0.29	0.43	0.26	0.02	0.00
1996	0.00	0.21	0.30	0.35	0.13	0.00

Predicted Fishery Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.02	0.08	0.26	0.45	0.17	0.02
1986	0.02	0.08	0.29	0.41	0.18	0.01
1987	0.03	0.10	0.28	0.43	0.15	0.01
1988	0.04	0.13	0.32	0.36	0.14	0.01
1989	0.07	0.18	0.35	0.31	0.09	0.01
1990	0.07	0.24	0.39	0.24	0.06	0.00
1991	0.06	0.25	0.42	0.23	0.04	0.00
1992	0.07	0.25	0.44	0.20	0.03	0.00
1993	0.08	0.28	0.42	0.20	0.03	0.00
1994	0.07	0.25	0.48	0.18	0.02	0.00
1995	0.06	0.18	0.46	0.28	0.03	0.00
1996	0.04	0.13	0.38	0.39	0.07	0.00

Table 21. Observed and predicted fishery mature harvest age compositions.

Observed Mature Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.00	0.00	0.15	0.73	0.12	0.00
1986	0.00	0.00	0.00	0.41	0.59	0.00
1987	0.00	0.00	0.00	0.29	0.71	0.00
1988	0.00	0.00	0.02	0.40	0.57	0.01
1989	0.00	0.00	0.06	0.60	0.31	0.03
1990	0.00	0.13	0.29	0.42	0.16	0.00
1991	0.00	0.11	0.28	0.50	0.11	0.00
1992	0.00	0.08	0.19	0.49	0.25	0.00
1993	0.00	0.16	0.19	0.62	0.03	0.00
1994	0.00	0.04	0.23	0.66	0.07	0.00
1995	0.00	0.02	0.24	0.68	0.06	0.00
1996	0.00	0.02	0.24	0.68	0.06	0.00

Predicted Mature Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.00	0.00	0.08	0.53	0.35	0.04
1986	0.00	0.00	0.09	0.50	0.38	0.03
1987	0.00	0.01	0.09	0.54	0.33	0.03
1988	0.00	0.01	0.12	0.51	0.34	0.02
1989	0.00	0.01	0.16	0.54	0.27	0.02
1990	0.00	0.02	0.22	0.53	0.21	0.01
1991	0.00	0.03	0.26	0.55	0.16	0.01
1992	0.00	0.03	0.30	0.53	0.14	0.00
1993	0.00	0.03	0.30	0.54	0.12	0.00
1994	0.00	0.03	0.35	0.50	0.11	0.00
1995	0.00	0.02	0.26	0.61	0.11	0.00
1996	0.00	0.01	0.16	0.64	0.18	0.00

Table 22. Observed and predicted weir harvest age compositions.

Observed Weir Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.00	0.06	0.17	0.60	0.16	0.01
1986	0.00	0.02	0.07	0.62	0.29	0.00
1987	0.00	0.12	0.12	0.40	0.33	0.03
1988	0.00	0.18	0.16	0.53	0.12	0.00
1989	0.00	0.23	0.13	0.39	0.25	0.00
1990	0.00	0.29	0.22	0.34	0.14	0.00
1991	0.00	0.35	0.43	0.21	0.01	0.00
1992	0.00	0.28	0.43	0.27	0.02	0.00
1993	0.00	0.28	0.46	0.25	0.02	0.00
1994	0.00	0.21	0.68	0.11	0.00	0.00
1995	0.00	0.20	0.45	0.35	0.01	0.00
1996	0.00	0.20	0.45	0.35	0.01	0.00

Predicted Weir Harvest Age Composition

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
1985	0.01	0.06	0.21	0.48	0.22	0.02
1986	0.01	0.05	0.24	0.45	0.23	0.02
1987	0.02	0.07	0.24	0.47	0.19	0.02
1988	0.02	0.09	0.28	0.41	0.19	0.01
1989	0.04	0.13	0.32	0.37	0.13	0.01
1990	0.04	0.18	0.37	0.31	0.09	0.01
1991	0.04	0.20	0.40	0.30	0.06	0.00
1992	0.05	0.20	0.43	0.27	0.05	0.00
1993	0.05	0.22	0.41	0.27	0.04	0.00
1994	0.05	0.19	0.47	0.24	0.04	0.00
1995	0.04	0.13	0.43	0.36	0.04	0.00
1996	0.02	0.09	0.32	0.47	0.09	0.00

Table 23. Parameter estimates from a sensitivity analysis on age-0 baseline natural mortality. Age-0 natural mortality was increased by 25% from an intitial value of 0.75 to 0.94.

Parameter	Value
Fishing Intensity	
f_{1985}	0.462
f_{1986}	0.597
f_{1987}	0.548
f_{1988}	0.434
f_{1989}	0.409
f_{1990}	0.274
f_{1991}	0.311
f_{1992}	0.228
f_{1993}	0.233
f_{1994}	0.220
f_{1995}	0.226
f_{1996}	0.223
Selectivity	
α	1.784
β	2.576
Maturation	
α	1.909
β	2.978

Parameter	Value
TVM	
γ_{1985}	0.002
γ_{1986}	0.003
γ_{1987}	0.457
γ_{1988}	0.590
γ_{1989}	1.021
γ_{1990}	0.871
γ_{1991}	1.384
γ_{1992}	1.472
γ_{1993}	1.651
γ_{1994}	1.145
γ_{1995}	0.495
γ_{1996}	0.239
α	31.325
β	1.183
Catchability Coefficient	
q	7.406E-08

Table 24. Parameter estimates from a sensitivity analysis on age-0 baseline natural mortality. Age-0 natural mortality was decreased by 25% from an intitial value of 0.75 to 0.56.

Parameter	Value	Parameter	Value
Fishing Intensity		*TVM*	
f_{1985}	0.309	γ_{1985}	0.000
f_{1986}	0.456	γ_{1986}	0.338
f_{1987}	0.420	γ_{1987}	0.418
f_{1988}	0.325	γ_{1988}	0.678
f_{1989}	0.310	γ_{1989}	1.087
f_{1990}	0.207	γ_{1990}	0.932
f_{1991}	0.233	γ_{1991}	1.420
f_{1992}	0.172	γ_{1992}	1.510
f_{1993}	0.175	γ_{1993}	1.695
f_{1994}	0.166	γ_{1994}	1.177
f_{1995}	0.171	γ_{1995}	0.555
f_{1996}	0.168	γ_{1996}	0.291
		α	41.752
Selectivity		β	1.468
α	1.755		
β	2.642	*Catchability Coefficient*	
		q	5.592E-08
Maturation			
α	1.910		
β	2.947		

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