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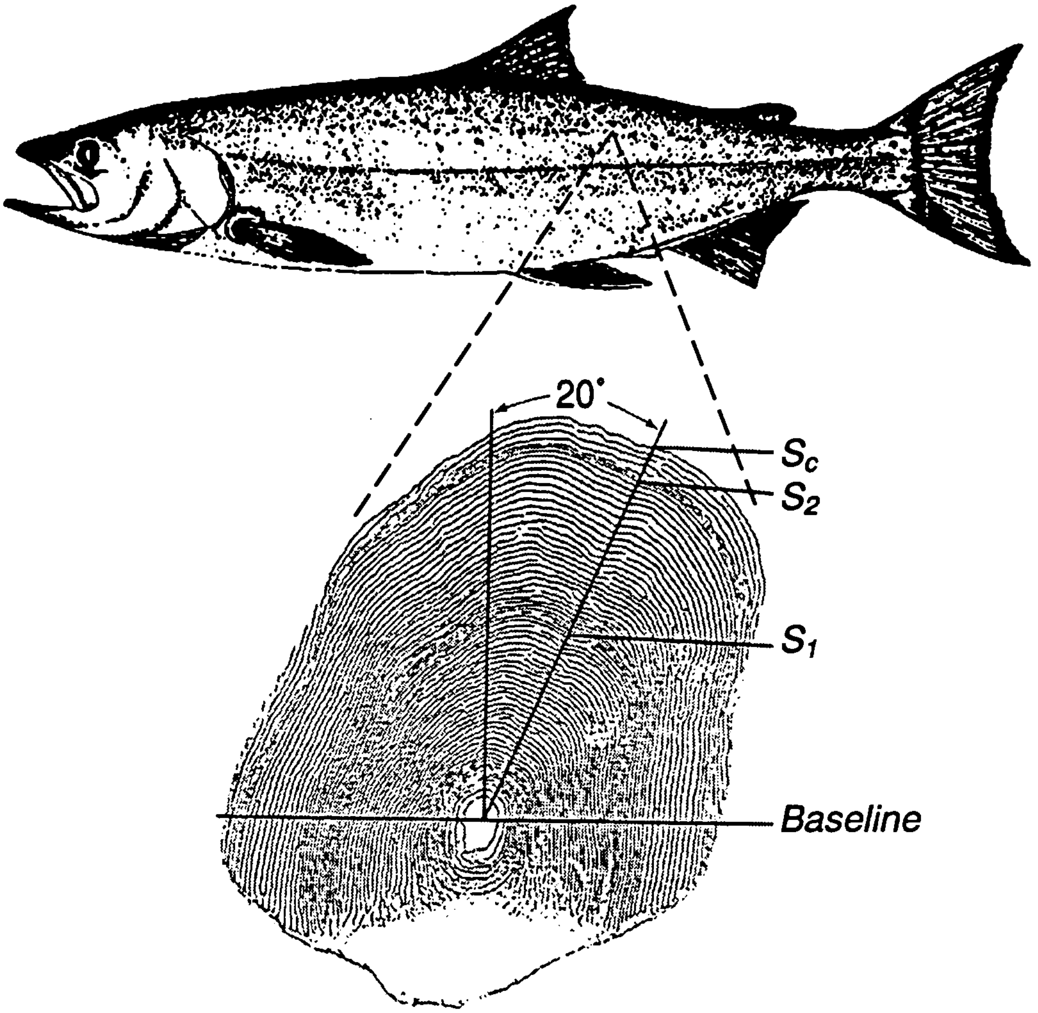
Age and Growth of Chinook Salmon in Lake Michigan: Verification, Current Analysis, and Past Trends

Jay K. Wesley



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AGE AND GROWTH OF CHINOOK SALMON IN LAKE MICHIGAN: VERIFICATION, CURRENT ANALYSIS, AND PAST TRENDS

by

Jay K. Wesley

A thesis submitted in partial fulfillment
of the requirements for the degree of
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Committee members

Associate Professor James S. Diana, chairman

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ABSTRACT

Chinook salmon *Oncorhynchus tshawytscha* from the Lake Michigan sport fishery were studied to determine if changes in age and growth occurred with recent forage shifts from alewife *Alosa pseudoharengus* to bloater chub *Coregonus hoyi*. A decrease in growth may indicate that forage shift stress caused the outbreak of bacterial kidney disease (BKD) *Renibacterium salmoninarum*. Known age chinook salmon implanted with coded-wire tags were collected in 1994 to validate aging techniques and to compare growth between fish collected by anglers and gill nets. Scale and vertebra aging were 95.6% and 93.9% accurate, respectively. There were no differences in age, gender, and maturity specific mean back calculated lengths (mm) between harvest gears. There was also no difference in mean back calculated length between sexes; however, immature age-0.2 fish were smaller than mature age-0.2 fish. Mean back calculated total lengths and Fulton Indices of condition were used to analyze historic growth using data and scales from the Michigan Department of Natural Resources Lake Michigan Creel Survey from 1983 to 1993. Average age decreased from a high in 1986 of 2.59 years to a low of 1.53 years in 1993. Mean length and condition declined recently for age 0.1. Mean length increased from 1983 to 1993 for age 0.3. Condition increased after BKD for age 0.3 and 0.4 chinook salmon. The increase in length and condition of age 0.3 and 0.4 chinook salmon may be a competitive release and/or size differential mortality in response to BKD. A reduction of chinook salmon stocking in Lake Michigan might restore growth and reduce mortality associated with BKD.

ACKNOWLEDGMENTS

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CHAPTER ONE

Introduction

Chinook salmon *Oncorhynchus tshawytscha* were first introduced into the Laurentian Great Lakes along with other salmonids as early as 1873 (Parsons 1973). These early introductions of chinook were unsuccessful. Native predators such as lake trout *Salvelinus namaycush*, burbot *Lota lota*, and walleye *Stizostedion virtreum* presumably out competed the chinook salmon (Carl 1980), and sustained in stable populations until the 1940s. At this time, the sea lamprey *Petromyzon marinus* became established and began to forage upon the large predators. Sea lamprey predation coupled with overexploitation from the commercial fishery severely reduced the predator base. With the lack of predators and the high harvest reducing several chub species in abundance, the exotic alewife *Alosa pseudoharengus* population expanded unchecked by competitors or predators. Sea lamprey control was initiated in 1960 (Smith 1968). With lower levels of sea lamprey and a large prey biomass of alewives, fishery managers began stocking lake trout in 1965 followed by coho salmon *O. kisutch* in 1966 and chinook salmon in 1967 (Smith 1968 and Parsons 1973). The intent of this salmon stocking was to utilize the abundant alewife and to increase the potential for recreational fishing (Tody and Tanner 1966). The stocking was instrumental in creating the most spectacular sport fishery in Lake Michigan's history (Keller et al. 1990).

Introductions of chinook salmon in Lake Michigan began with about 700,000 during the late 1960's (Parsons 1973). Stocking levels peaked in 1989 at 7,859,000 and then decreased to roughly 5,500,00 in the early 1990s (Holey 1995). These hatchery produced fish also occurred with naturally produced chinook salmon in Lake Michigan, as Hesse (1994) estimated 30% of the age 1 and 2 chinook salmon harvested by anglers between 1992 and 1993 were naturally produced.

Sport catch rates (fish per 100 angler hours) of chinook salmon in the Michigan waters of Lake Michigan peaked in 1986 at 10.26 and declined to a record low of 1.80 in 1993 (Rakoczy and Svoboda 1994). Much of this decline was due to high mortality associated with bacterial kidney disease (BKD) caused by *Renibacterium salmoninarum* which was first detected in high numbers of Lake Michigan chinook salmon in 1988 (Nelson and Hnath 1990, Johnson and Hnath 1991). Although BKD mainly appears to infect hatchery fish, it has been detected in low numbers of naturally produced chinook salmon (Maclean and Yoder 1970, Nelson and Hnath 1990). However, Hesse (1994) found no significant difference in the incidence of BKD between hatchery and naturally produced chinook salmon. Incidence of BKD has remained high since 1988, and Rybicki (1994) observed an incidence of BKD between 21.6 and 59.4 percent for all age groups combined from 1990 through 1993.

MacLean and Yoder (1970) reported that there was low incidence of BKD in coho salmon and chinook salmon as early as 1967 in Michigan waters. Heavy mortalities associated with BKD occurred in several hatcheries at that time. These high mortalities usually occurred after a stress such as declines in dissolved oxygen, algal blooms, or changes in diet. The stressor appeared to reduce resistance to the disease allowing its further development. BKD rarely causes mortality unless accompanied by a stress (Maclean and Yoder 1970, Nelson and Hnath 1990).

It has been hypothesized that the outbreak of BKD was due to a recent shift in forage biomass in Lake Michigan. Brown et al. (1994) described a change in Lake Michigan's forage community from predominately alewife to bloater chub *Coregonus hoyi.* Stewart et al. (1981), Stewart and Ibarra (1991), and Jones et al. (1993) have documented interactions between forage fishes and salmonids using bioenergetic models and predicted diet shifts and decreased growth in chinook salmon. Increased search time for forage (Jones et al. 1993) and changing diet other than high energy alewife (Stewart and Ibarra 1991) may decrease total energy consumption of chinook salmon which would lead to stress. Perhaps this stress from alewife declines caused the high mortalities associated with BKD since 1988 (Nelson and Hnath 1990).

If stress due to forage conditions was a factor in the BKD outbreak, the evaluation of growth rates may reveal this potential stress. If growth declined prior to the onset of BKD, this would support the concept that available forage declines caused the outbreak. If there was no change in growth, this fails to support that concept and may indicate other factors as important to BKD outbreak, such as increased concentrations of disease organisms in the water caused by release of infected fish from hatcheries. Hansen (1986) found a decline in condition and trophy size (95th percentile weight) of chinook salmon in the southern basin of Lake

Michigan beginning in 1975; however, his evaluation of condition and weight were not age specific. Growth analyses before and after the onset of BKD are not available, and analyses related to size at capture in the sport fishery (Rakoczy 1992) or size at return to harvest weirs (Hay 1992) do not directly address growth rate. Sport fishery and weir harvest data do not incorporate good estimates of age, and a change in size may just be a shift in age distribution and not necessarily a difference in growth. Growth data collected from the weirs for chinook salmon were based on ages determined by length frequencies because erosion in the scales makes direct aging impossible.

A verified and accurate analysis of age and growth of chinook salmon in Lake Michigan would be useful to evaluate one potential cause of BKD, stress due to forage change. Good growth analyses will also improve management decisions regarding chinook salmon and reliability of bioenergetic models. Improved aging techniques for Lake Michigan chinook will also improve future growth analyses.

Goal and Objectives

The goal of this project was to assess the age and growth of chinook salmon in the Michigan waters of Lake Michigan. This goal involved three objectives: 1) to accurately determine and validate ages of chinook salmon taken from Lake Michigan, including fish caught by anglers and those taken by Michigan Department of Natural Resources (MDNR) surveys; 2) to use age and size data to estimate growth rates of chinook salmon in Lake Michigan based on year class, sex, and maturity; 3) to use historical data to determine ages and growth rates of chinook salmon and compare them to current ages and growth rates.

This thesis is divided into four chapters. Chapter 2 addresses the development of the aging method and its validation. Chapter 3 describes the growth of chinook salmon at large in Lake Michigan. Chapter 4 applies growth analyses to historical chinook age and growth data using techniques developed in chapters 2 and 3 and compares past and present growth rates.

CHAPTER TWO

The Development and Validation of an Accurate Aging Technique for Chinook Salmon from Lake Michigan

Introduction

In order to evaluate growth of chinook salmon in Lake Michigan, accurate aging techniques need to be applied. A count of growth zones in calcified fish structures have been used to determine age for many species. These calcified structures have included otoliths (Pannella 1971, Nielson and Geen 1982), dorsal spines (Chilton and Bilton 1986), pectoral fin rays (Rien and Beamederfer 1994), vertebrae (Appelget and Smith 1951, Prince et al. 1985, Hesse 1994), opercula (McConnell 1951), cleithra (Harrison and Hadley 1979), and scales (LaLanne and Safsten 1969, Berg 1978, Seelbach and Beyerle 1984, Sharp and Bernard 1988, Baker and Timmons 1991). Concerns for validation of aging fish with bony structures were raised by Beamish and McFarlane (1983), and since then several bony structures have been validated for a variety of fish (Matlock et al. 1987, Sharp and Bernard 1988, Baker and Timmons 1991, Ferreira and Russ 1994 , Hesse 1994, and Rien and Beamederfer 1994). The most direct tests of validity compare structures to known age fish. Known age fish can be raised in captivity or marked and released into a natural environment and recaptured (Weatherley and Gill 1987). Tags are best for marking because each marked fish can be individually identified. Other methods for estimation of fish age include length frequency and modal progression analyses

(Tesch 1968). Scales have been used most often to age chinook salmon in Lake Michigan because scales are easily sampled from fish and can be stored efficiently.

Chinook salmon scales have been reported difficult to age with confidence. Godfrey et al. (1968) determined an accuracy of 75% using scales from chinook salmon harvested in the Pacific Ocean. Validity of scale aging sexually mature chinook salmon harvested in Lake Michigan had been questioned (Dan Anson, Personal Communication). Hay (1992) also expressed the difficulty in aging chinook salmon harvested at blocking weirs during spawning migration. Therefore, there is a need to validate the scale aging technique and to determine the accuracy of scale aging by different individuals before any growth analysis can be attempted. The objective of this chapter is to develop and validate an accurate scale aging technique for chinook salmon in Lake Michigan using known ages. Vertebrae were also analyzed, tested for aging accuracy, and compared to work by Hesse (1994).

Methods

Sample Source

Chinook salmon released as smolts to Lake Michigan in 1990 to 1994 were marked with coded-wire tags (CWT) and adipose fin clip by Michigan DNR personnel. The absence of the adipose fin was used by anglers and agency personnel to identify tagged fish. For this study, anglers from Lake Michigan were sampled by myself and personnel from U.S. Fish and Wildlife Service. Known age chinook salmon were also collected from MDNR experimental gill nets and the Ludington

Pumped Storage assessment gill nets. Total length (to 1 mm), weight (to 1 g), sex, gonad development, scales, vertebrae, visual checks for BKD, and noses (cut just behind the eye) containing CWTs were collected from all fish. Gonad development data consisted of visual inspections to determine if gonads were mature or immature. Immature gonads were small, colorless, and laid close to the vertebral column. Mature gonads were enlarged, colorful (orange for ovaries and white for testes), and filled the body cavity. Scales were sampled between the dorsal and adipose fins above the lateral line as described by Scarnecchia (1979). Five to fifteen vertebrae were collected between the adipose fin and the caudal peduncle. The presence of BKD was identified by a swollen kidney and/or white pustules (MacLean and Yoder 1970). Scales were stored in scale envelopes, while vertebrae and noses were kept frozen.

Laboratory Preparation

Coded-wire tags were analyzed by MDNR personnel at the Great Lakes Charlevoix Station; the year of stocking was determined for each fish by extracting the tag and reading the binary code. Vertebrae were prepared and aged using techniques developed by Hesse (1994). Flesh and cartilage were removed from the center of each vertebra. One to two vertebrae from each fish were covered with several drops of glycerin and viewed in a dark room through a dissecting scope, with a magnification of 15 to 40X, under ultraviolet light (365 nm). Impressions of 6 to 15 scales for each fish were made on acetate film. Several clean and non-regenerated scales were viewed on a microprojection apparatus (Lagler 1977) at a magnification of 40X to determine age.

Age was determined by counting the number of annuli from focus to edge of each scale. A lake annulus consisted of a close grouping of circuli with evidence of crossing over of the circuli (Figure 1). Smolt checks, which consisted of a close grouping of circuli located about 7 to 14 circuli from the focus, were not considered as lake annuli. A stream annulus was a close grouping of circuli, with clear evidence of crossing over following a tight band of 14 to 21 circuli from the focus (Carl 1980). In subsequent text, ages are represented using an Arabic number for stream annuli followed by a period and ending with another Arabic number for lake annuli (Godfrey et al. 1968, Seelbach and Beyerle 1984). For example, a three-year-old salmon which spent one year in a stream and two years in the lake was designated as age 1.2. The samples used for validating scale ages were all hatchery produced, so only lake years were present on these scales. Examples of age 0.2, 0.3, and 0.4 chinook salmon are illustrated in Figures 2, 3, and 4.

The timing of annulus formation was an important criterion to identify for accurate aging of chinook salmon in the spring. Fish caught in early spring may not have formed their last annulus prior to capture (Figure 5). For all such fish collected, one year was added to their scale age. The timing of annulus formation was determined by counting the number of fish exhibiting an initiated and completed annulus during the months of May through August.

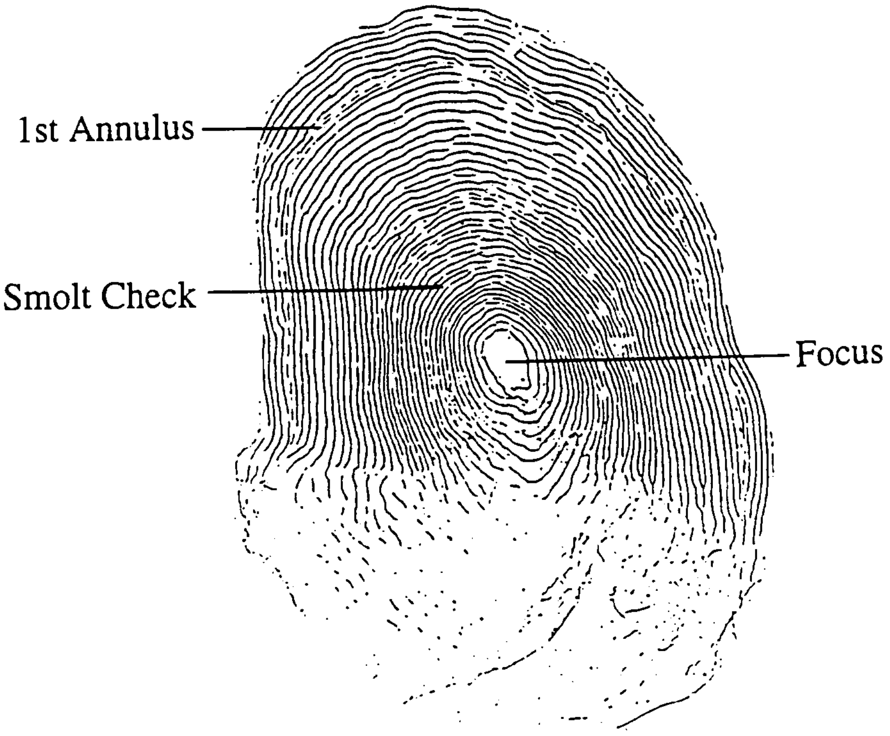

Figure 1. The image of a scale from an age 0.1 chinook salmon taken from the Lake Michigan sport fishery showing the focus, smolt check, and 1st annulus. Scale sample taken on 22 August 1994 (20x magnification).

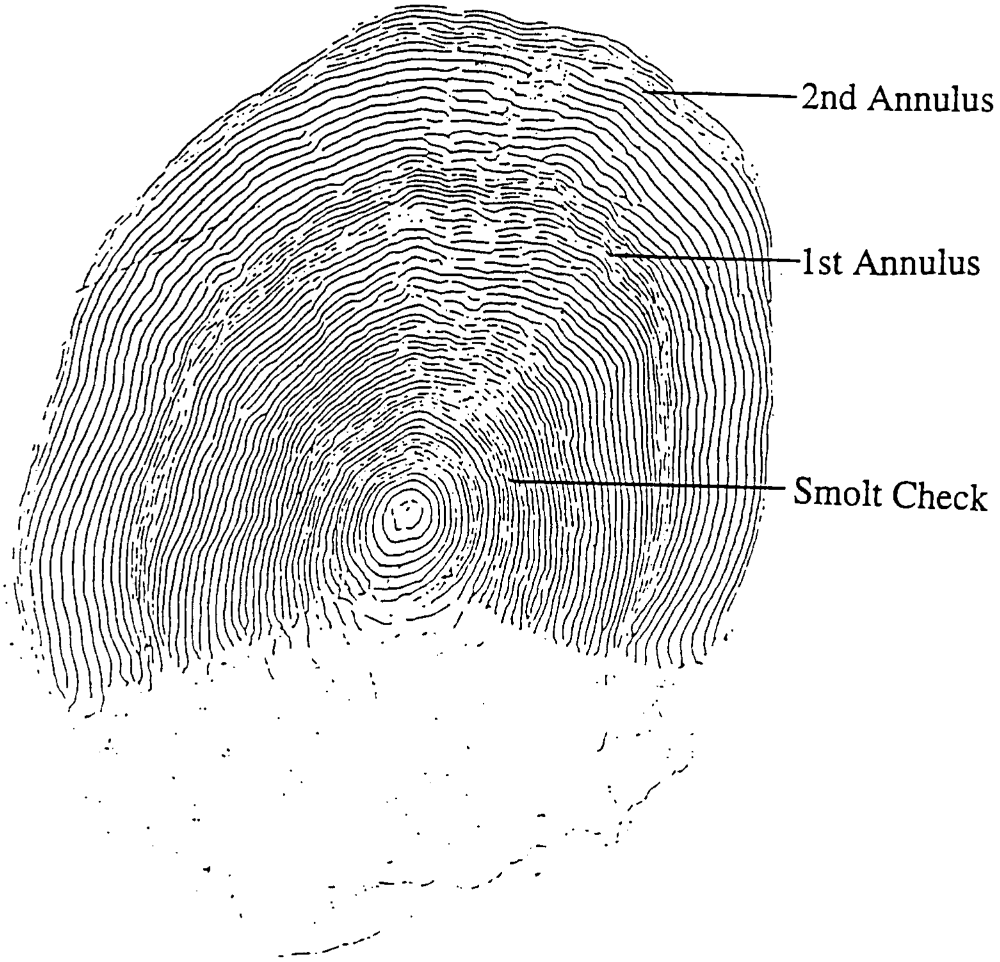

Figure 2. Magnified image of an age 0.2 scale taken from a chinook salmon in the Lake Michigan sport fishery on 23 August 1994 (20x magnification).

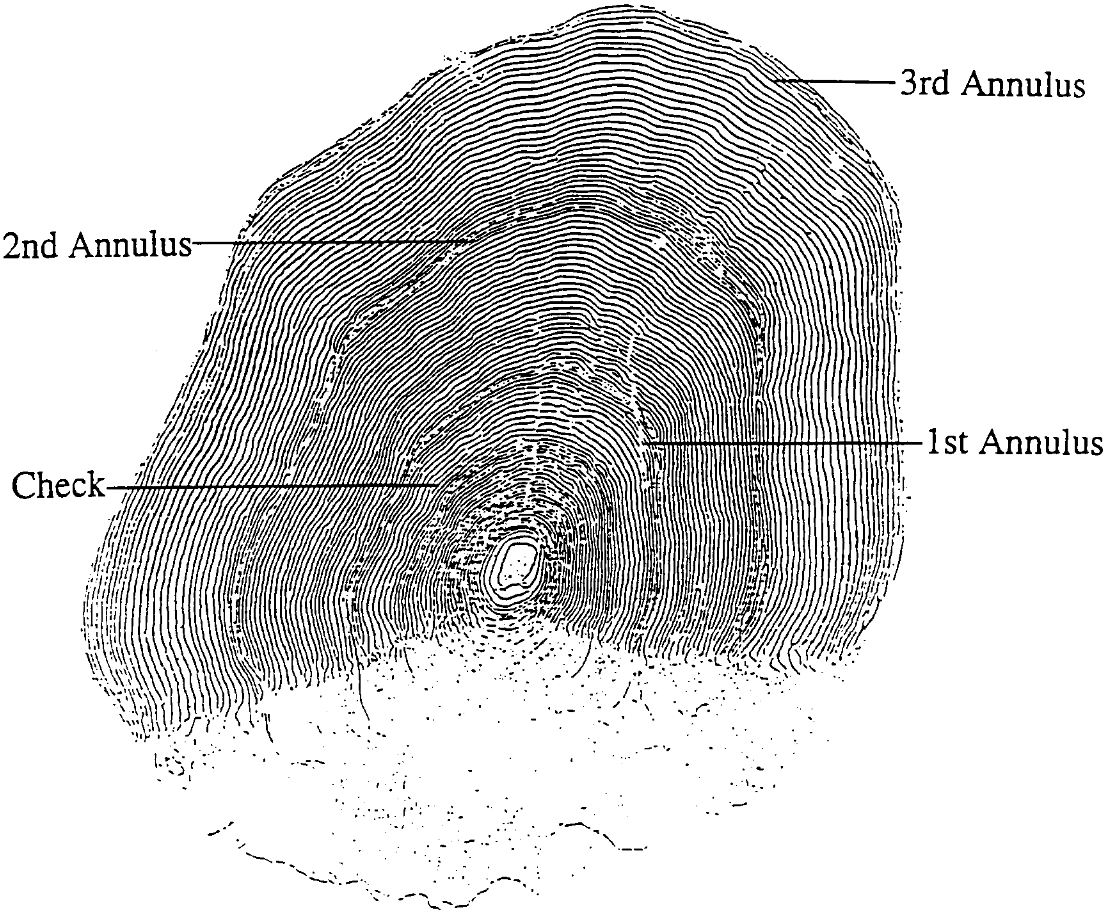

Figure 3. Magnified image of an age 0.3 scale taken from a chinook salmon in the Lake Michigan sport fishery on 10 July 1994 (10x magnification).

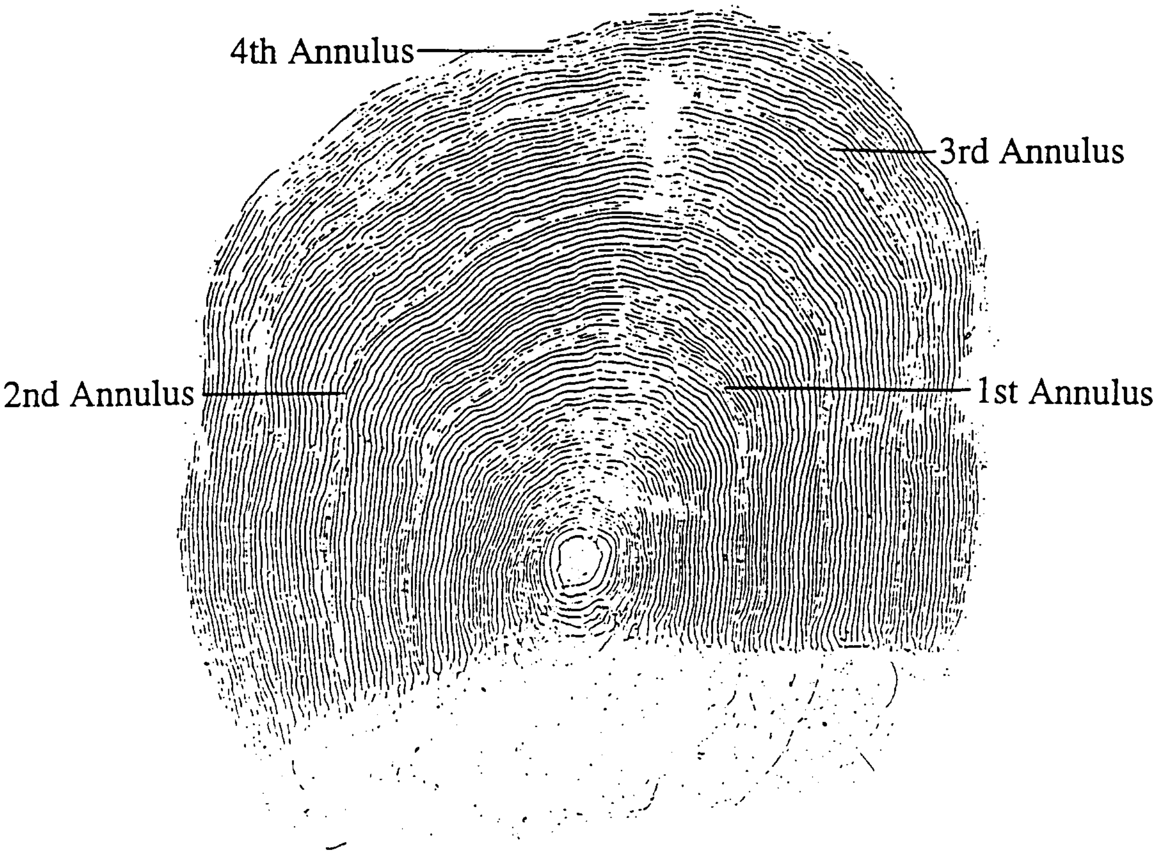

Figure 4. Magnified image of an age 0.4 scale taken from a chinook salmon in the Lake Michigan sport fishery on 1 June 1994 (10x magnification).

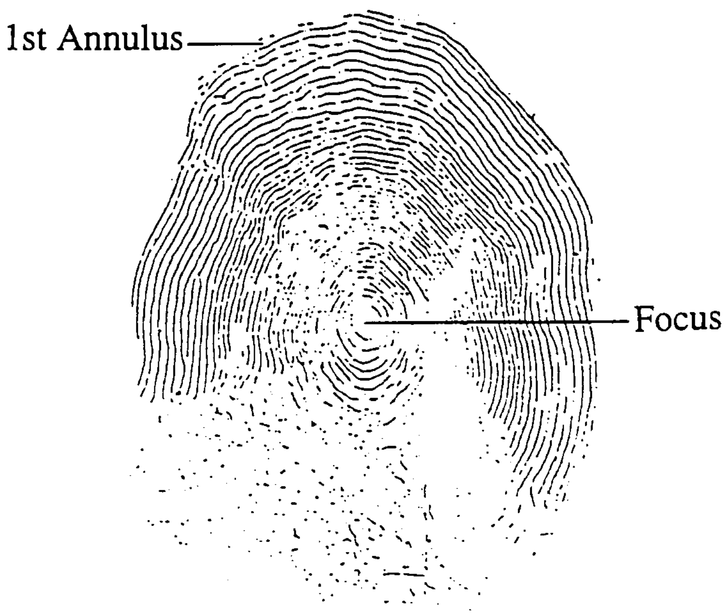

Figure 5. Magnified image of an age 0.1 scale taken from a chinook salmon in the Lake Michigan sport fishery on 7 May 1994, with the first annulus just visible on the scale margin (20x magnification).

Recognition of scale erosion is also important in aging chinook salmon. Scale erosion occurred in mature chinook salmon returning to the rivers to spawn. Eroded scales were characterized by the presence of a jagged edge on the scale and the loss of portions of the posterior margin of the scale (Figure 6 and 7). Scale erosion of salmon is caused by the resorption of nutrients which are used for energy to migrate upstream and for development of gonads (Wallin 1957). Resorption of the scale could erode past one or more annuli, causing an underestimate in age. Scales exhibiting erosion were not used in this analysis.

A pretrial was conducted to age chinook salmon which had CWT marks and known ages. After this pretrial, it was determined that fish size could influence scale age and bias estimates. Sizes of different age chinook salmon frequently overlapped, adding to aging error. Scales were organized by time of harvest from spring to fall and not by size class. Ordering by time of harvest allows the progession of annulus formation to be observed and limits biases related to size.

Accuracy and precision estimates for scale ages

Scale ages were compared to known ages to determine aging accuracy. The percent of fish aged correctly was calculated for all ages separately and also combined ages. The distribution of misaged chinook salmon was analyzed based on sex of fish and maturity. A similar procedure was performed for vertebrae.

The precision or repeatability between scale readers was estimated using statistical methods described by Beamish and Fournier (1981) and Chang (1982). Three scale readers (other than myself) independently aged the same sample of 76

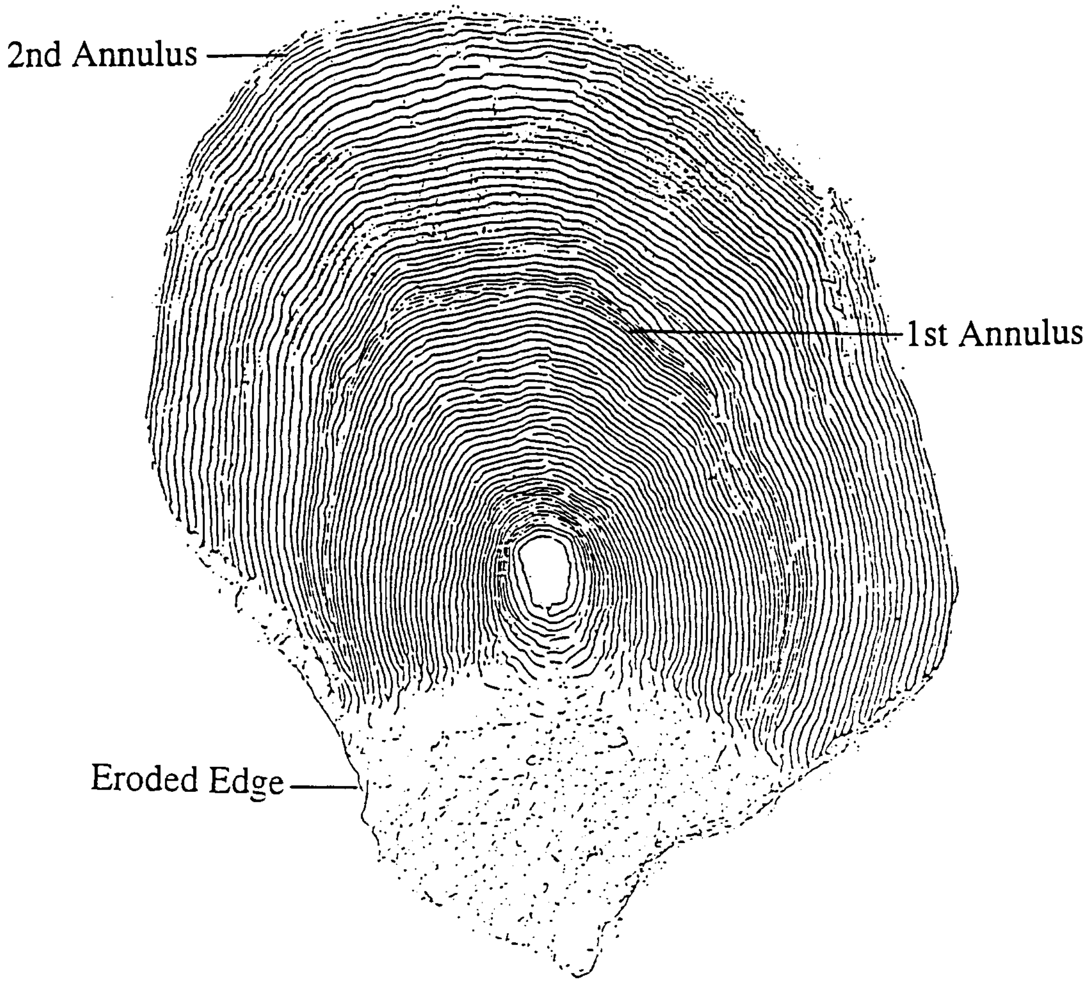

Figure 6. Magnified image of an age 0.2 scale taken from a chinook salmon in the Lake Michigan sport fishery on 27 August 1994, showing extensive erosion on the posterior margin (20x magnification).

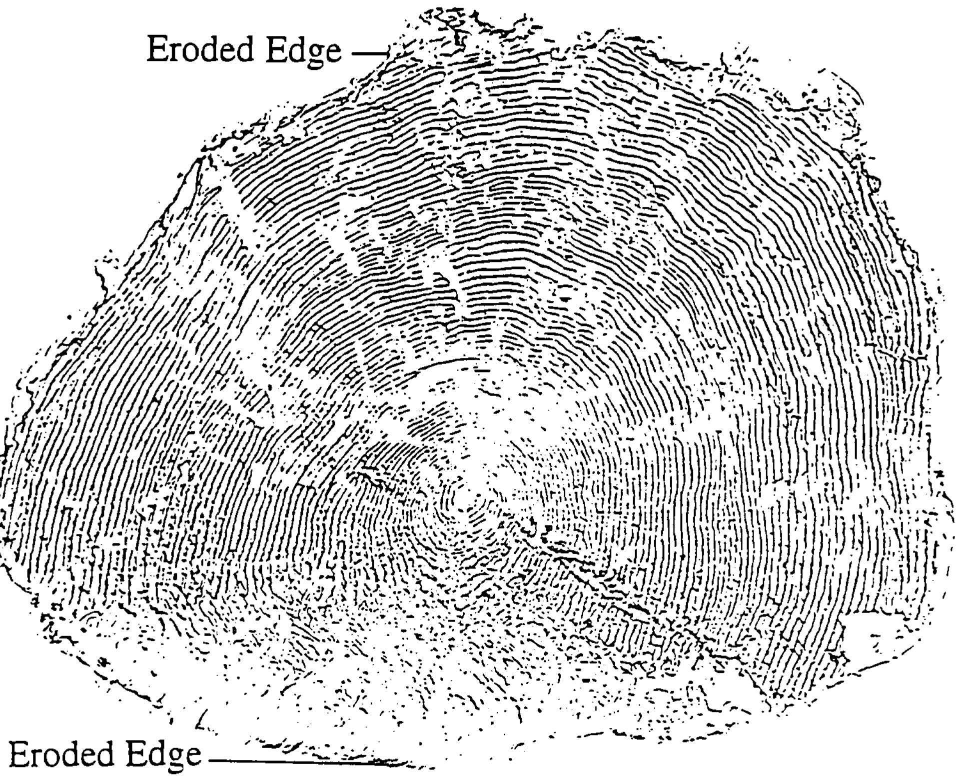

Figure 7. Magnified image of a severely eroded chinook salmon scale from the fall river sport fishery, 20 September 1994 (15x magnification).

scales containing fish of ages 0.1 through age 0.3. The readers were aware of the timing of annulus formation and were given time of harvest. Each reader used their own prefered method of aging chinook scales; therefore, precision was estimated for chinook salmon scales in general and not for my method of aging. These results were used to calculate the average percent error (*APE*), coefficient of variation (*V*), and index of precision (*D*). The average percent error was calculated using the number of fish aged (*N*), the number of scale readers (*R*), the *i*th age of the *j*th fish (X_{ij}), and the average age for the *j*th fish (X_j) using the equation:

$$APE = \frac{100}{N}\sum_{i=1}^{N}\left[\frac{1}{R}\sum_{j=1}^{R}\frac{\left|X_{ij} - X_j\right|}{X_j}\right]$$

V was calculated as the standard deviation divided by the mean for each fish, then was averaged for all fish and represented as a percentage. *D* was obtained by dividing *V* by the square root of *R*.

Results

A total of 302 chinook salmon were sampled from Lake Michigan between May and September 1994 from my sport fishery sampling (152), U.S. Fish and Wildlife Service sport fishery assessment (43), Ludington Pumped Storage assessment gill nets (12), and Michigan DNR gillnets (95). Of the 302 samples, 206 were used for scale analysis and 181 for vertebra analysis. Tag loss (fish exhibiting an adipose fin clip with no CWT) and inability to collect certain data in the field reduced the total samples collected to what could be used for each analysis. Fish exhibiting scale erosion were also excluded from analysis.

Chinook salmon in Lake Michigan began to form an annulus on the outer scale margin between mid-May and June, and 64.0 % of the sample had started annulus formation by June (Table 1 and Figure 8). The annulus was completely formed in 88.2 % of the sample by the end of July. Age 0.1 and 0.2 chinook salmon appeared to complete annulus formation earlier than age 0.3. Only 50.0 % of the age 0.3 fish exhibited a complete annulus formation by the end of July; however, the sample size was two. There was also a decline in the percentage of fish with complete annulus formation in August and September, with values of 85.7 % and 66.7 %, respectively.

Scale erosion was present in 14 of 83 fish collected between July and mid-September (Table 2). All of these fish with eroded scales were mature and ranged from age 0.2 to 0.4, and 71.4 % were males. Most of these fish (71.4%) were caught in August. Some were harvested near river mouths by anglers, but all were taken from Lake Michigan proper.

Accuracy and Precision

A total of 206 CWT chinook salmon was aged using scales. The overall accuracy was 95.6 %, and all age classes appeared to be aged with equal accuracy (Table 3). Aging 0.4 chinook salmon had 100 % accuracy; however, there was only a sample size of two. Errors in aging never exceeded one year (Table 4). Misaged chinook salmon were most commonly males (88% of the fish misaged)(Table 5);

Table 1. Timing of annulus formation in scales of chinook salmon from Lake Michigan. Samples include coded-wire tagged chinook salmon from the 1994 sport fishery and Ludington Pumped Storage Assessment gill nets.

Age	Percent showing start of annulus formation	Percent with annulus formation completed	Sample size
May			
1.0	26.7	0.0	15
2.0	41.2	5.9	17
3.0	25.0	0.0	4
4.0	...	...	0
Total:	33.3	2.8	36
June			
1.0	61.9	9.5	21
2.0	68.6	12.5	16
3.0	100.0	0.0	1
4.0	0.0	0.0	1
Total:	64.0	10.3	39
July			
1.0	100.0	87.5	8
2.0	100.0	100.0	7
3.0	100.0	50.0	2
4.0	...	...	0
Total:	100.0	88.2	17
August			
1.0	95.2	85.0	21
2.0	100.0	90.0	10
3.0	100.0	75.0	4
4.0	...	...	0
Total:	97.1	85.7	35
Sept.			
1.0	100.0	100.0	1
2.0	100.0	75.0	4
3.0	...	...	0
4.0	100.0	0.0	1
Total:	100.0	66.7	6

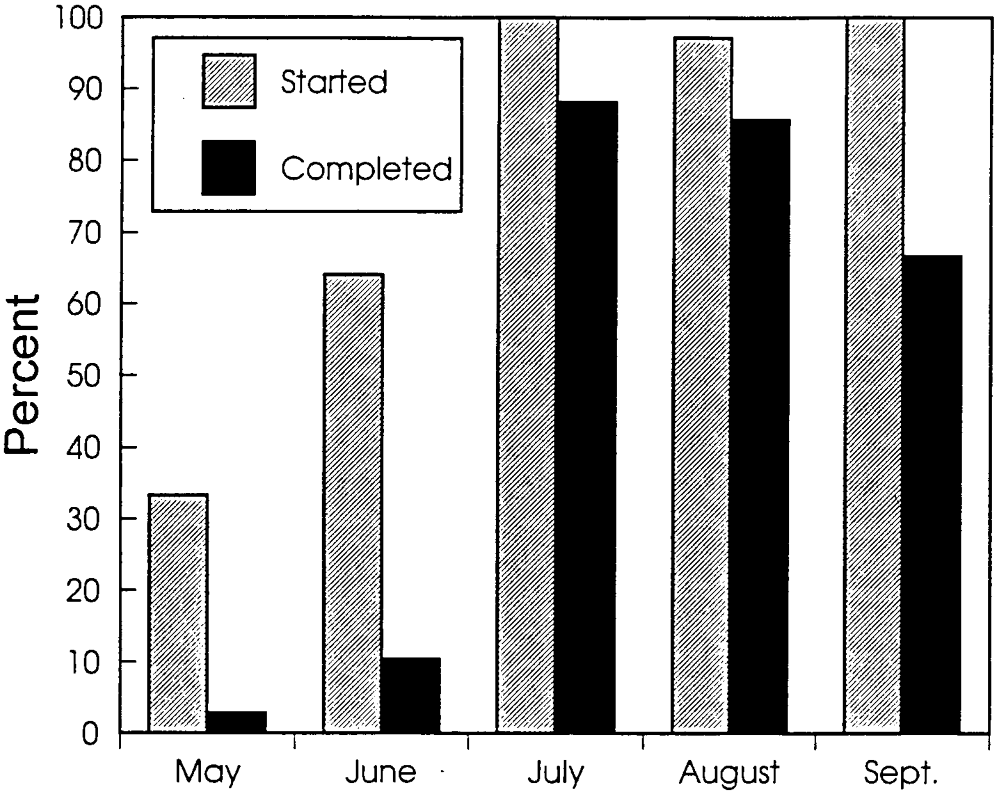

Figure 8. Percent of chinook salmon having started and completed scale annulus formation by month for fish taken from Lake Michigan in 1994.

Table 2. The percent and number of the total collected chinook salmon (in parenthesis) showing scale erosion reported by age, sex, and month.

	July		August		September	
Age	male	female	male	female	male	female
0.1	0.0 (5)	0.0 (6)	0.0 (19)	0.0 (10)	0.0 (1)	0.0 (1)
0.2	0.0 (3)	0.0 (4)	50.0 (6)	0.0 (4)	50.0 (4)	.... (0)
0.3	100.0 (1)	0.0 (5)	66.7 (3)	44.4 (9)	.... (0)	.... (0)
0.4	.... (0)	.... (0)	100.0 (1)	.... (0)	100.0 (1)	.... (0)
Total	11.1 (9)	0.0 (15)	20.7 (29)	17.4 (23)	50.0 (6)	0.0 (1)

Table 3. Scale aging accuracy for collected CWT chinook salmon.

Age	Sample Size	# Correct	% Correct	# Misaged	% Error
0.1	92	89	96.7	3	3.3
0.2	96	91	94.8	5	5.2
0.3	16	15	93.8	1	6.2
0.4	2	2	100.0	0	0.0
Total	206	197	95.6	9	4.4

Table 4. Differences between known age and age estimated by scales for CWT fish that were misaged.

CWT Age	Scale Age	Frequency		Error in age (yr)
		Scale<CWT	Scale>CWT	
0.1	0.2	0	3	+1
0.2	0.1	2	0	-1
0.2	0.3	0	3	+1
0.3	0.2	1	0	-1

Table 5. Distribution of the percent of misaged chinook salmon scales based on maturity and gender.

	Mature	Immature	Total
Male	44.4 (4)	44.4 (4)	88.8 (8)
Female	11.1 (1)	..... (0)	11.1 (1)
Total	55.5 (5)	44.4 (4)	

however, there was no significant difference in misaging frequency between sex and maturity (p=0.342) based on Pearson's Chi-square statistic.

The accuracy of aging for all age classes of CWT chinook salmon using vertebrae was 93.9 % with a sample size of 181 (Table 6). Age 0.1 chinook salmon were the most accurately aged (100%), while age 0.4 had the lowest accuracy of aging (50%). Again, there was only a sample size of two for age 0.4 chinook salmon. Differences between known and estimated ages never exceeded one year (Table 7). Males were misaged more often than females, and more immature fish were misaged than mature fish (Table 8). Most of these immature fish were small fish of the age 0.2 year class. There was no significant difference, however, between sex and maturity (p=0.425, Pearson's Chi-square) based on misaged chinook salmon using vertebrae.

There were 10 discrepancies assigning age among the three scale readers in the estimate of precision (Table 9). The index of APE calculated to be 3.63 %. The V and D calculated to be 4.80 % and 2.77 %, respectively.

Discussion

Use of inaccurate ages may cause serious errors in fish population management. Beamish and McFarlane (1983) further list the significance of validation for aging methods. I have demonstrated that scale and vertebrae aging can be used accurately for age 0.1, 0.2, and 0.3 chinook salmon from Lake Michigan. My accuracy of aging vertebrae agrees with the results of Hesse (1994). However, the ability to accurately determine age for age 0.4 chinook salmon still remains a question using either scales or vertebrae. Due to the small sample size of known-aged fish, I

Table 6. Vertebra aging accuracy of collected CWT chinook salmon sampled.

Age	Sample Size	# Correct	% Correct	# Misaged	% Error
0.1	77	77	100.0	0	0.0
0.2	87	79	90.8	8	9.2
0.3	15	13	86.7	2	13.3
0.4	2	1	50.0	1	50.0
Total	181	170	93.9	11	6.1

Table 7. Differences between known age and age estimated by vertebrae for CWT fish that were misaged.

CWT Age	Vertebra Age	Frequency		Error in age (yr)
		Vert<CWT	Vert>CWT	
0.2	0.1	7	0	-1
0.2	0.3	0	2	+1
0.3	0.2	1	0	-1

Table 8. Distribution of the percent of misaged chinook salmon vertebrae based on maturity and gender.

	Mature	Immature	Total
Male	9.1 (1)	63.6[a] (7)	72.7 (8)
Female	9.1 (1)	18.2 (2)	27.3 (3)
Total	18.2 (2)	81.8 (9)	

[a] mostly small sized 0.2 year olds

Table 9. Estimated scale ages and associated *APE*, *V*, and *D* of 3 readers who each analyzed scales from 76 chinook salmon taken in Lake Michigan.

n	Known Age	Estimated Age Reader 1	Reader 2	Reader 3	*APE*	*V*	*D*
21	1	1	1	1	0	0	0
38	2	2	2	2	0	0	0
7	3	3	3	3	0	0	0
2	1	1	1	2	0.3333	0.4330	0.2500
4	1	1	2	1	0.3333	0.4330	0.2500
1	2	1	2	2	0.2666	0.3464	0.2000
1	2	1	3	2	0.3333	0.5000	0.2887
1	3	2	2	3	0.1905	0.2474	0.1429
1	2	3	3	2	0.1667	0.2165	0.1250
				Avg.%	3.63	4.80	2.77

could not determine accuracy of age 0.4 fish with confidence. Age 0.4 chinook salmon probably represent a small percentage of the total population in Lake Michigan based on angler harvest, but the large size of age 0.4 chinook salmon is important to the fishery (Rakoczy and Svoboda 1994).

Scale aging of chinook salmon is more accurate for fish taken from Lake Michigan than from the Pacific Ocean. Godfrey et al. (1968) found that scales were only 75 % accurate using chinook salmon from Columbia River. This decreased accuracy can be accounted for by the more complex life history of chinook salmon in Columbia River and the lack of information used by the scale readers. Godfrey et al. (1968) states that chinook salmon may spend several years in the river before migrating to the ocean and may not return to rivers for up to six years. This life history is much more variable than for chinook salmon in Lake Michigan. The scale readers in that study also knew only that chinook salmon scales were being read, not any information related to annulus formation dates.

Knowledge of the timing of annulus formation, recognition of scale erosion, awareness of smolt checks, and the use of information such as date of harvest can help increase scale aging accuracy. The timing of the annulus formation is important when aging fish harvested in spring, as the last annulus may not be formed until late May to July. Scales exhibiting erosion should not be aged with confidence due to the potential loss of annuli causing underestimation of age. For these reasons, harvest date is important information to know about an individual fish. Harvest date indicates whether a formed annulus will be present at the scale margin. In initial aging, it is also beneficial to order a sample by date collected from spring to fall so that the progression of annulus formation can be followed. Ordering by date also reduces potential biases associated with ordering scale samples by size of fish. For example, lengths of age 0.0 chinook salmon in the fall overlap with age 0.1 chinook salmon in the spring. If date of harvest is not considered, age 0.1 fish in the spring can easily be confused with age 0.0 fish in the fall because neither show an annulus formation.

Most error in aging chinook salmon from Lake Michigan using scales occurred on males and with fish age 0.2, which may be due to varying growth in these groups causing unusual scale characteristics. Fast growing fish are typically easier to age because there are wide areas in the scale between annuli. If this fast growth occurs in the spring, recognition of an annulus may become more difficult due to fewer circuli being closely grouped. In these cases, it is also important to find crossing over of the circuli.

Aging with vertebrae was also accurate, with overall accuracy (93.9%) being slightly lower than scale accuracy (95.6%). Vertebral aging accuracy was also slightly lower in this study than the estimate of 95.4% made by Hesse (1994) using lake harvested chinook salmon. Like scale aging error, most vertebrae aging error was with males. However, more vertebrae from immature chinook salmon were misaged compared to mature fish. Most of these errors were small sized fish of the age 0.2 year class. These small age 0.2 vertebrae may not have strong areas with opaque and translucent zones (Hesse 1994), or zones representing the first annulus might be confused with smolt checks. Although the same techniques were applied, different scopes and lab conditions were used by Hesse (1994) which may influence accuracy results. The low sample size of age 0.4 chinook vertebrae makes the aging accuracy using vertebrae of age 0.4 fish still in question.

Scale aging of chinook salmon from Lake Michigan also appears to be precise based on comparative results of three readers. The resulting 3.63 % *APE* and 4.80 % *V* are relatively low, and low values of *APE* and *V* indicate high precision or repeatability between readers (Beamish and Fournier 1981, Chang 1982). The *D* value shows that an average of 2.77 % of the total error was contributed by each observation of age (Chang 1982).

Precision of scale aging and vertebrae aging are equal based on three readers. There was no significant difference between my scale aging and vertebrae aging precision estimates made by Hesse (1994) based on *APE*, *V*, and *D* ($p>0.05$, t-tests). Differences in age assignment rarely deviated from one year with chinook salmon. If errors frequently departed one or two years in age, this would indicate poor precision because chinook salmon only live up to five years in Lake Michigan.

The following set protocol for aging chinook salmon from Lake Michigan incorporates life history complexity and its effect on aging: 1) An annulus consists of a close grouping of circuli with evidence of crossing over of the circuli. 2) A smolt check is a close grouping of circuli about 7 to 14 circuli counts from the focus. 3) A stream annulus is a close grouping of circuli with evidence of crossing over of the circuli after a tight band of 14 to 21 circuli from the focus followed by a smolt check (Carl 1980). 4) Annulus formation occurs between May and July. 5) Scales exhibiting erosion should be eliminated from analysis. 6) Vertebrae should be used as an alternative to scales for mature fish harvested in Lake Michigan and at blocking harvest weirs in the fall.

There are many advantages to using scales for aging fish. Two main advantages are the ease of sampling and handling, as well as the ability to return fish alive once scales have been removed. In addition estimates of growth can easily be made from scales using back calculation. Finally, there are historical collections of scales which can be reanalyzed. The main disadvantage of scales in aging chinook salmon is that scale erosion occurs in the fall. Most mature chinook salmon harvested after August exhibited scale erosion, and this is a large disadvantage because chinook become more vulnerable to angling in the fall as they stage to migrate. Weir harvested scales are also very difficult to age because of scale erosion.

Hesse (1994) explained the advantages and disadvantages of aging with vertebrae. The most important advantage of using vertebrae is that erosion or distortion does not occur to vertebrae. Vertebrae can be used to age mature chinook salmon harvested in the fall sport fishery and at weirs.

Based on the young age and fast growth of chinook salmon in Lake Michigan, it is expected that aging of their bony structures would be accurate and precise. Lake trout, which are slow growing and live as long as 20 years (Becker 1983), are more difficult to age. Growth declines with age making annuli difficult to identify in bony structures such as scales in lake trout (Johnson 1976, Sharp and Bernard 1988). However, aging of chinook salmon becomes more difficult with a complex life history. Most temperate fishes form an annulus once a year during slow growth in winter (Tesch 1968). Chinook salmon also exhibited smolt checks in bony structures, which are produced during slow growth periods while migrating downstream. Annuli in chinook salmon usually occur after the smolt check but may occur before in stream yearlings (Carl 1980, Seelbach and Beyerle 1984). Within Lake Michigan, chinook salmon show variation in growth and age at maturity and mature fish returning to natal streams using resorb energy stored in body parts including scales. This complexity in the life history of chinook salmon along with the late annulus formation can make aging difficult. The suggested aging protocol with scales and vertebrae should decrease this difficulty and is a valid technique.

CHAPTER THREE

Growth Rate by Age, Sex, and Maturity Classes of Chinook Salmon in Lake Michigan

Introduction

Knowledge of fish growth can be useful in assessing the health of individuals and populations of fish. Understanding the factors that influence growth are also important in comparing different populations of the same species. These factors, which include abiotic factors (such as temperature, oxygen, salinity, and light) and biotic factors (such as ration, fish density, competition, predation, food abundance, and food availability) are reviewed in Tesch (1968), Weatherley and Gill (1987), and Diana (1995). Because of these factors, growth can vary with season and life history characteristics such as maturity, sex, and age (Weatherley and Gill 1987).

Pacific salmon can have very complicated life histories (Chapter Two). Healey (1991) summarized life history observations of chinook salmon from the Pacific Ocean. Male chinook salmon tend to have more rapid growth and mature earlier than females. Based on MDNR weir data, male chinook salmon in Lake Michigan also grow faster and mature earlier than females (Hay 1992, Pecor 1992). However, there is little data on age-specific growth of chinook salmon, as well as growth differences based on gender or maturity. Chapter Two evaluated an accurate aging system, including validation with CWT fish, to use on fish at large in Lake Michigan. This allows an accurate evaluation of growth differences among different age classes, gender, and maturity. Growth rates can be determined with confidence because there will be no age misclassification; therefore, the differences in growth can be associated with the particular life history characteristics. One main purpose of this chapter is to investigate current growth rates in chinook salmon at large in Lake Michigan.

The methods for analyzing growth are many. These methods can be grouped into the following categories: 1) static analysis or the comparison of mean size of each cohort once in a year; 2) cohort analysis or determining mean size of each cohort several times during the year; 3) individual analysis which involves measuring the change in size of marked individuals; and 4) back calculation which uses bony parts to calculate growth history (Bagenal and Tesch 1978, Casselman 1987, Diana 1995). The method of back calculation will be emphasized in this and the following Chapter.

Back calculation is a technique of inferring a fish's length using a set of measurements made on bony structures. Tesch (1968), Weatherley and Gill (1987), and Francis (1990) give thorough reviews of the historic and current methods used in back calculation as well as the types of calcified structures measured. The use of back calculation can increase the amount of length-at-age data (Shafi and Jasim 1982) and allows estimation of lengths at ages rarely observed for some species (Francis 1990). Growth rates obtained from back calculated lengths have also been used to compare cohorts (Frost and Kipling 1980) and to relate growth due to various physical and biological factors (Weatherley and Gill 1987). Most back calculation methods use a relationship between the body length and scale radius of the fish. This can be a linear or curved relationship (Tesch 1968, Weatherley and Gill 1987, Francis

1990). The Fraser-Lee method (Hile 1970, Carlander 1981, Frie 1982) requires a linear relationship and uses this line to calculate the intercept which is described as the length of the fish at scale formation. The method uses the proportion of body length to scale length for each fish to back calculate individual length, which is an advantage because it allows variation between individuals unlike regression methods (Carlander 1981). Carlander (1949) cautions that variation in scales can lead to error in body-scale relationships. A comparison of lengths at capture avoids errors due to body-scale relationship but creates problems due to differences in time of capture. Another common problem with back calculation is Lee's Phenomenon, which occurs when computed lengths at a given age are smaller than observed lengths. Lee's phenomenon is more pronounced when calculating lengths of young fish from much older fish (Tesch 1968). These problems can be avoided by calculating lengths only to the last annulus which offers a more valid method for comparative purposed (Carlander 1949).

The second purpose of this chapter is to compare growth rates between sport harvested and gill net harvested chinook salmon in Lake Michigan. It is common to group these two sampling methods to increase sample size. With decreased abundance and catches of age 0.3 and age 0.4 chinook salmon, it may be necessary to combine different harvesting methods to increase sample size. However, these methods of harvesting may select different size chinook salmon which could bias growth analyses. For example, Miranda et al. (1987) found anglers caught longer largemouth bass *Micropterus salmoides* than did electrofishing or cove rotenone sampling. Anglers appear to catch the largest fish of each cohort. They may also catch the most aggressive fish, which may have faster growth rates than a typical fish from that population (Quinn and Unwin 1993). Therefore, before the two collections can be combined, it is important to compare the two collecting methods for sampling bias.

The main objective of this chapter is to compare current growth of chinook salmon from Lake Michigan between fish with different life history characteristics such as age, sex, and maturation state. The second objective is to compare lengths of chinook salmon from two different sampling gears, angler and gill net harvests. Both objectives involved back calculation using scales.

Methods

Sample Source and Preparation

Coded-wire tagged (CWT) chinook salmon as described in Chapter Two were sampled from the eastern Lake Michigan sport fishery and MDNR *R.V. Steelhead* gill nets between May and September 1994. Sport fishery and gill net samples were combined from each port to create one sport fishery sample and one gill net sample for the entire year. Gill net samples came from the eastern shoreline of Lake Michigan from New Buffalo in the south to Little Traverse Bay in the north (Figure 9). Chinook salmon were targeted during spring in the south (May), summer in central (June),and fall in the north (July-August) region of Lake Michigan. Gill nets consisted of 9-m deep monofilament twine with mesh sizes of 9 cm to 16.5 cm with a 2.5 cm interval (Rybicki 1995).

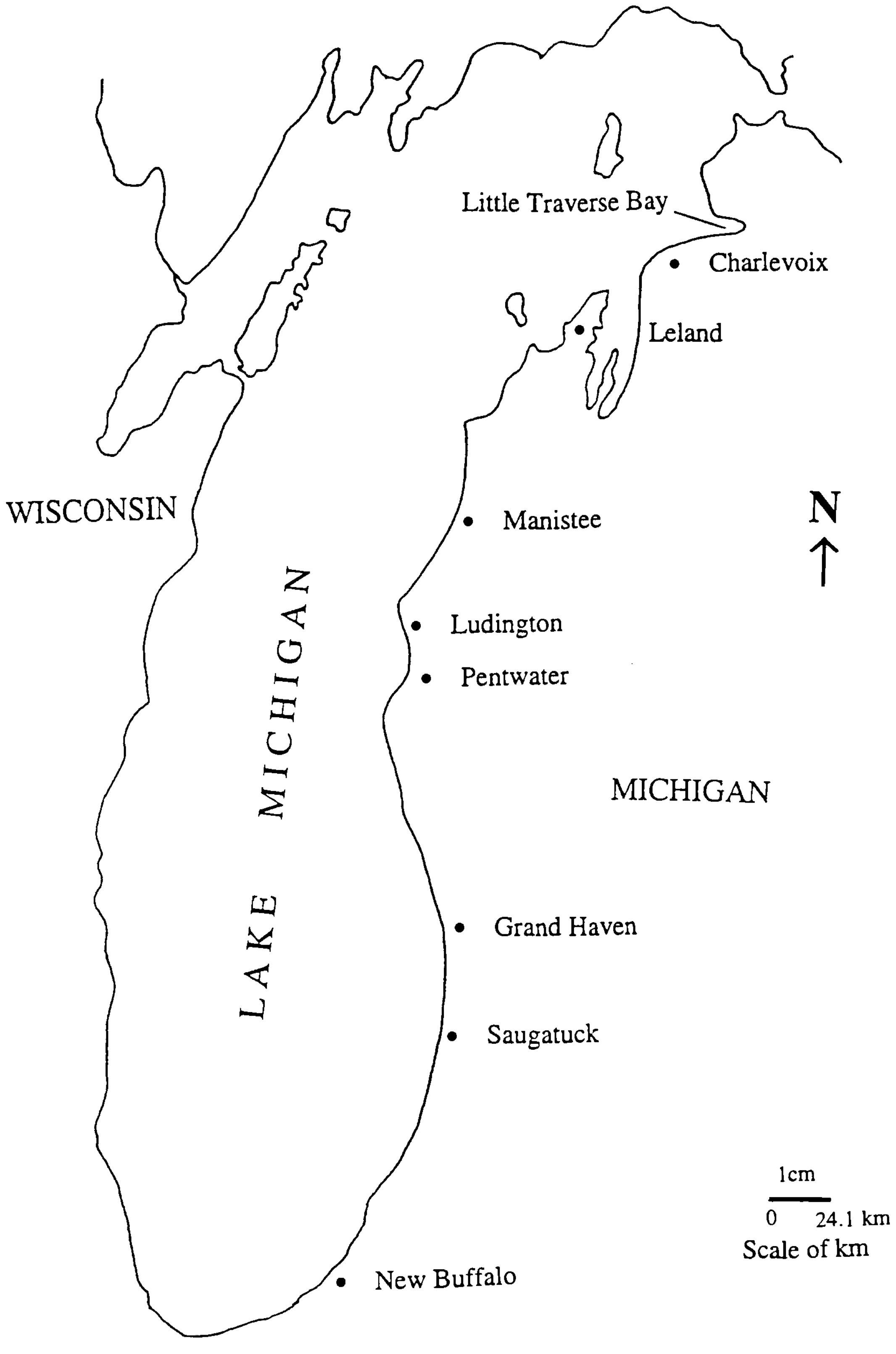

Figure 9. A map of Lake Michigan and location of sampled ports.

The sport fishery was sampled from Saugatuck in the south to Leland in the north (Figure 9). Port selection was dependent on chinook salmon catch; therefore, ports were frequently sampled if catch rates of chinook salmon were high compared to the rest of eastern Lake Michigan. Targeted areas at each port included cleaning stations where angler concentrations were high. Data were collected by myself or by trained volunteers from all observed CWT fish.

Weight (to 1 g), total length (to 1 mm), sex, gonad development, scales (taken between the dorsal and adipose fins above the lateral line), visual checks for BKD (swelling and/or pustules in the kidney) and noses (cut just behind the eye) containing tags were collected. Immature gonads were described as small, colorless, and found close to the vertebral column, while mature gonads were enlarged, colorful (orange for ovaries and white for testes), and filled the body cavity. Known fish ages from CWTs were provided by MDNR. Scales were pressed in acetate film.

Growth Analysis

Back calculation of mean total length at age using scales was used to compare growth of sport and gill net harvested chinook salmon. Lengths were back calculated only to the last annulus not to previous annuli; therefore, the mean length of age 0.1 fish is the back calculated length to the 1st annulus of fish harvested at age 0.1 only. Similarly, mean length of age 0.2 is back calculated length to the 2nd annulus of fish harvested at age 0.2. Back calculating lengths to the last annulus avoids problems associated with Lee's phenomenon. The Faser-Lee method of back calculation was used (Hile 1970, Carlander 1981, Carlander 1982, and Frie 1982). This method required computation of the simple linear regression of fish length versus scale radius (1) used in the back calculation formula (2) to estimate total lengths as follows:

$$(1)\ L = a + b(S_c)$$

$$(2)\ L_i = a + \left[(L_c - a)\left(\frac{S_i}{S_c}\right)\right]$$

Where S_c is the scale measurement to the edge of the scale, L_c is the length of fish at capture, a is the intercept of the body-scale regression in equation (1), S_i is the scale measurement to the *i*th annulus, and L_i is the length of fish at the *i*th annulus.

An annulus was defined as close grouping of circuli with crossing over of the circuli (see Chapter Two and Figures 1-5). Measurements to each annuli and to the edge of the scale were made with a microcomputer Java projecting system (3x magnification) (Acker and Mitchell 1988). These measurements from the focus to the edge of the scale were made through the longest radius which was approximately 20° from the perpendicular axis of the scale (see Figure 10).

Separate regressions between total length and scale radii were calculated for fish harvested by sport or gill nets to estimate a in equation (1) which was then used in equation (2). Predicted total lengths from equation (2) were compared between chinook salmon harvested by sport and gill net. The mean back calculated total lengths of the two collecting methods were tested for equivalence using t-tests.

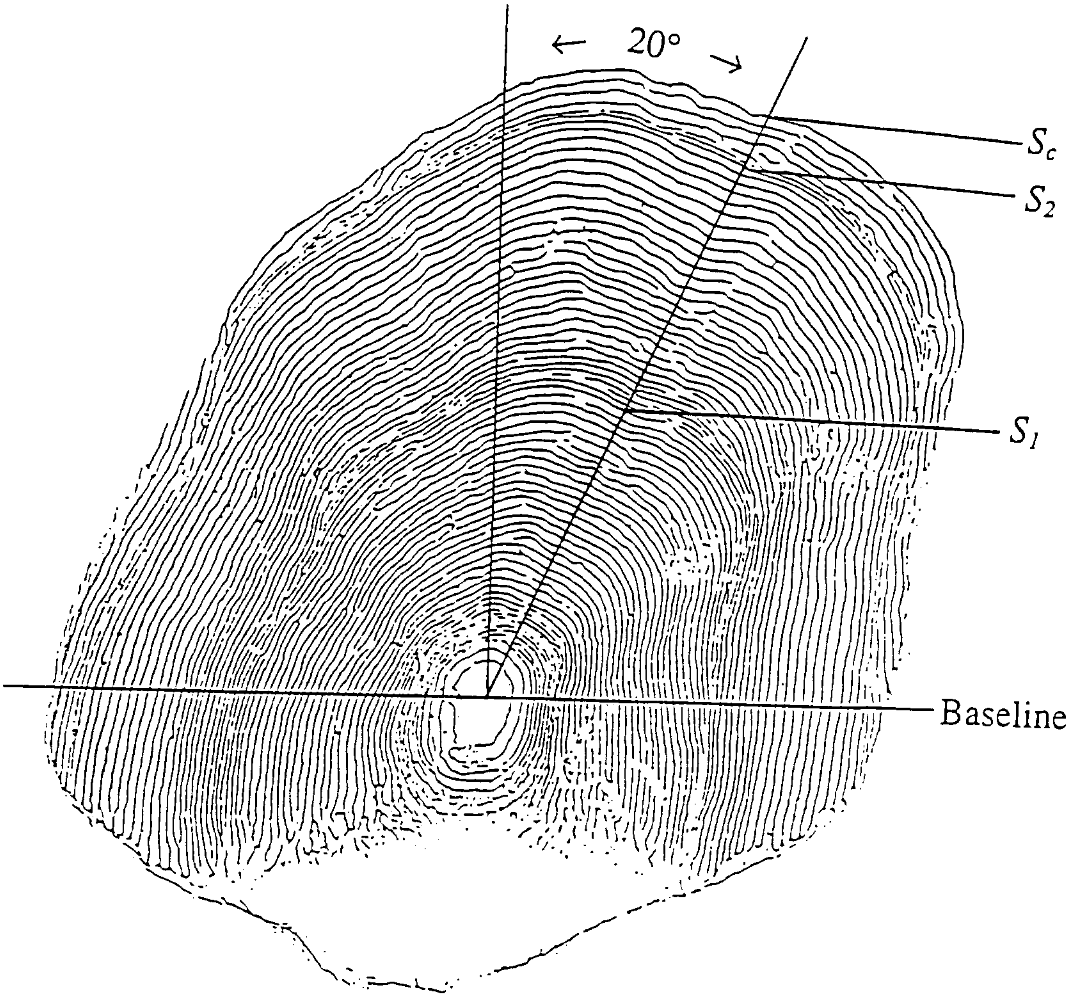

Figure 10. Illustration of a chinook salmon scale with measurements used in the Fraser-Lee back calculation formula. S_1 is the distance from the focus to the 1st annulus, S_2 is the distance from the focus to the 2nd annulus, and S_c is the distance from the focus to the scale edge. All measurements were taken at about 20° from the perpendicular axis of the scale (20x magnification).

Comparisons with t-tests were also made by age and gender. Assumptions of normality and equal variances were tested using coefficients of skewness, kurtosis, and F-tests for equal variance. All tests were run at the 5 % level of significance using SPSS (Norusis 1993).

Results

Scales and size data from a total of 130 sport and 75 netted fish were used to back calculate growth. Fish lengths and scale radii were plotted and regressed for sport harvested (Figure 11) and gill netted (Figure 12) chinook salmon. The equations in Figures 11 and 12 both had good linear relationships yielding R^2 values of 0.92 and 0.83, respectively.

The mean back calculation results (Table 10) based on age and gender met assumptions of normality and homogeneity. There were no significant differences in mean length between sport caught and gill netted chinook salmon for age 0.1 males, age 0.1 females, and age 0.3 females. There was a significant difference in mean length at age 0.2 for males and age 0.2 females between the two methods of harvest, with length being larger in gill netted fish. There were more mature age 0.2 males in the gill net harvest (n=11) than in the sport harvest (n=5).

There were no significant differences between mature or immature age 0.2 chinook salmon with the two sampling methods (Table 11). Immature males taken by a collection gear were significantly smaller than mature males. Mean length for immature age 0.2 females was also significantly lower than mature females for gill net

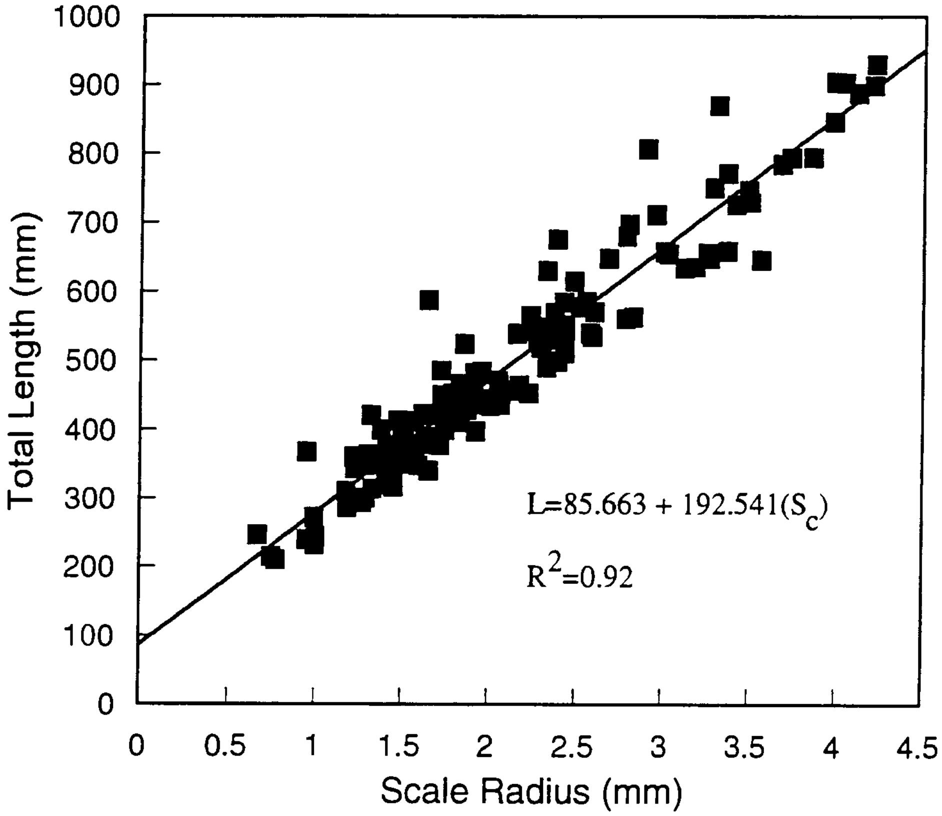

Figure 11. Plot of scale radius and fish total length for chinook salmon harvested by sport in Lake Michigan, 1994.

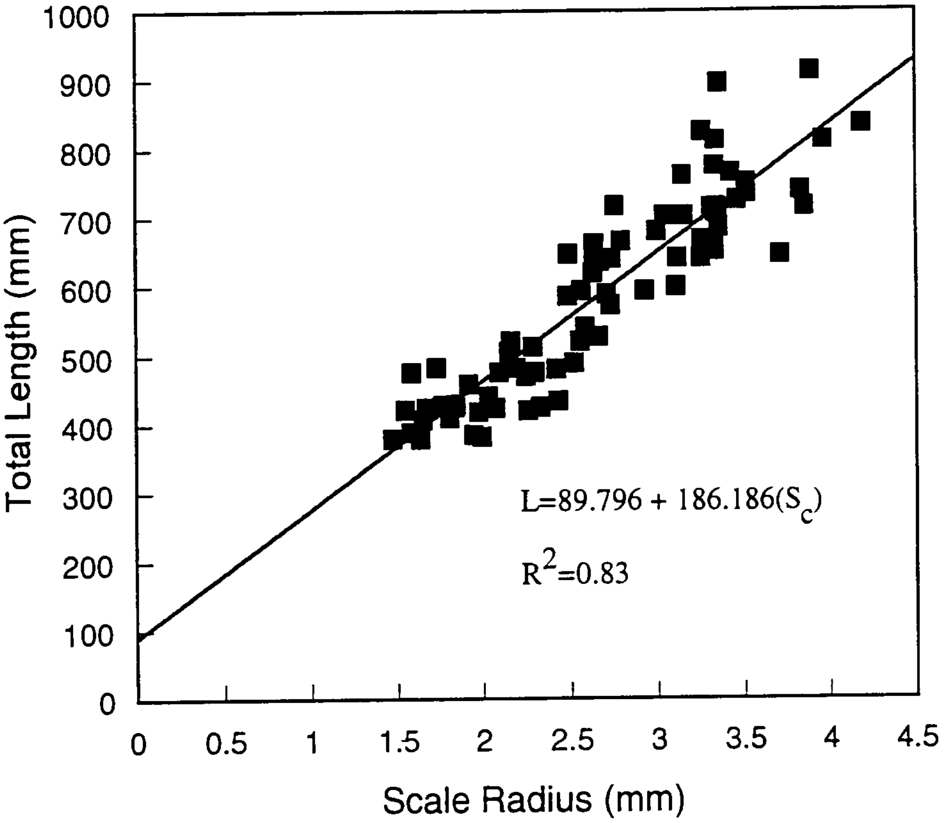

Figure 12. Plot of scale radius and fish total length for chinook salmon harvested by gill net in Lake Michigan, 1994.

Table 10. Age and gender specific mean back calculated total lengths (mm) for CWT chinook salmon from Lake Michigan harvested by anglers or gill net, 1994.

	Mean Total Length Males		
Age	Sport Catch	Gill Net	P Value
0.1	373.8	393.3	NS[a]
0.2	565.6	646.4	0.02
0.3	.....	823.5	.....
	Mean Total Length Females		
0.1	354.0	373.5	NS
0.2	565.0	622.2	0.02
0.3	790.2	791.4	NS

[a] No significant difference between collecting gears.

Table 11. Age 0.2 gender and maturity specific mean back calculated total lengths (mm) for sport and gill net harvested chinook salmon from Lake Michigan, 1994.

	Age 0.2 Males		
	Sport Catch	Gill Net	P Value
Immature	530.9	570.0	NS[a]
Mature	690.4[b]	688.1[c]	NS
	Age 0.2 Females		
Immature	565.0	581.5	NS
Mature	....	687.4[d]	....

[a] no significant difference between collecting gears.
[b] significant difference between sport caught mature and immature males ($p=0.001$).
[c] significant difference between gill netted mature and immature males ($p=0.01$).
[d] significant difference between gill netted mature and immature females ($p<0.001$).

harvested chinook. The sample size was too small for age 0.2 females to test sport caught females by maturity status.

Since the significant difference between harvest gears at age 0.2 in Table 10 is due to maturity composition of samples and not due to other harvest gear biases, the two samples were combined (Table 12). Again, immature males and females were significantly smaller in length than mature males and females.

Lengths were also back calculated to earlier ages (Table 13) to look at different growth trajectories based on life history traits. Yearly growth increments were plotted for females (Figure 13) and males (Figure 14). Mature males and females were larger in total length and had slightly higher slopes indicating better growth rates.

Discussion

Maturity is size related for chinook salmon in Lake Michigan since the largest members of the younger age classes matured (Figures 13 and 14). Males also seemed to mature at a younger age than females; however, there was no significant difference in total length between males and females. The maturity results agree with MDNR weir data (Hay 1992, Pecor 1992) and also with Healey's (1986) suggestion that male chinook salmon show more variation in size at maturity than females from Pacific populations. Berg (1978) also found no significant differences in age specific growth between sexes in chinook salmon from Lake Superior.

In general, age at maturity is inversely related to growth in salmon (Neilson and Geen 1986, Heath et al. 1991, Bohlin et al. 1994, Mangel 1994), charr (Matuszek

Table 12. Pooled age, gender, and maturity (I for immature; M for mature) specific mean back calculated total lengths (mm) for sport and gill net harvested chinook salmon from Lake Michigan, 1994.

Age	Maturity	Males	Females	p Value
0.1	I	381.2	363.3	NS[a]
0.2	I	545.9	573.6	NS
0.2	M	699.2[b]	687.4[c]	NS
0.3	I,M	849.4	783.6	NS

[a] no significant difference in mean length between males and females.

[b] significant difference in mean length of age 0.2 immature and mature males ($p<0.001$).

[c] significant difference in mean length of age 0.2 immature and mature females ($p<0.001$).

Table 13. Mean back calculated lengths (mm) at earlier age of chinook salmon from the Michigan waters of Lake Michigan based on gender and maturity.

Year Class	Age 0.1	Age 0.2	Age 0.3	Age 0.4
Immature Males				
1993	381.2			
1992	384.2	545.9		
Immature Females				
1993	363.3			
1992	386.7	573.6		
1991	369.3	551.7	662.2 *	
Mature Males				
1993	453.3 *			
1992	425.7	699.2		
1991	374.1	618.6	849.4	
1990	403.5	615.6	836.0	900.2 *
Mature Females				
1993	...			
1992	440.0	687.4		
1991	399.6	632.8	810.6	
1990	395.0	564.4	737.0	870.0 *

* sample size of one.

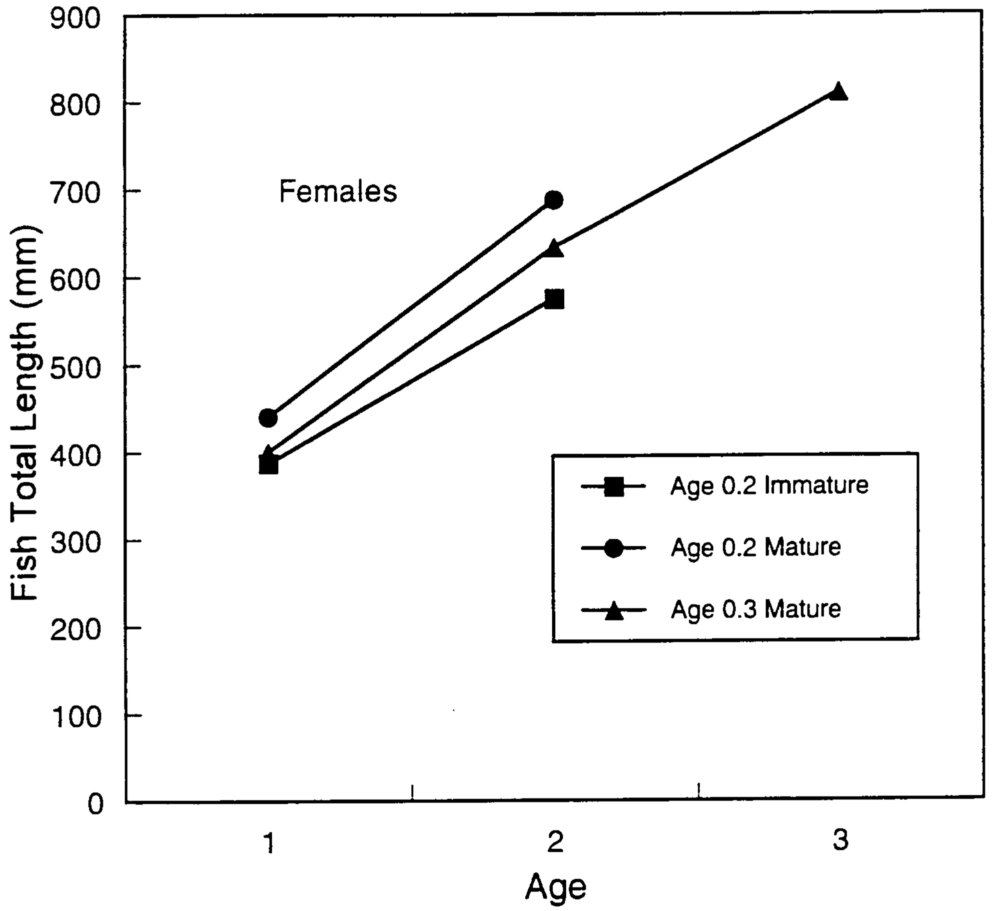

Figure 13. Lake Michigan chinook salmon back calculated annual growth increments for females based on total lengths of pooled sport and gill net harvested fish, 1994.

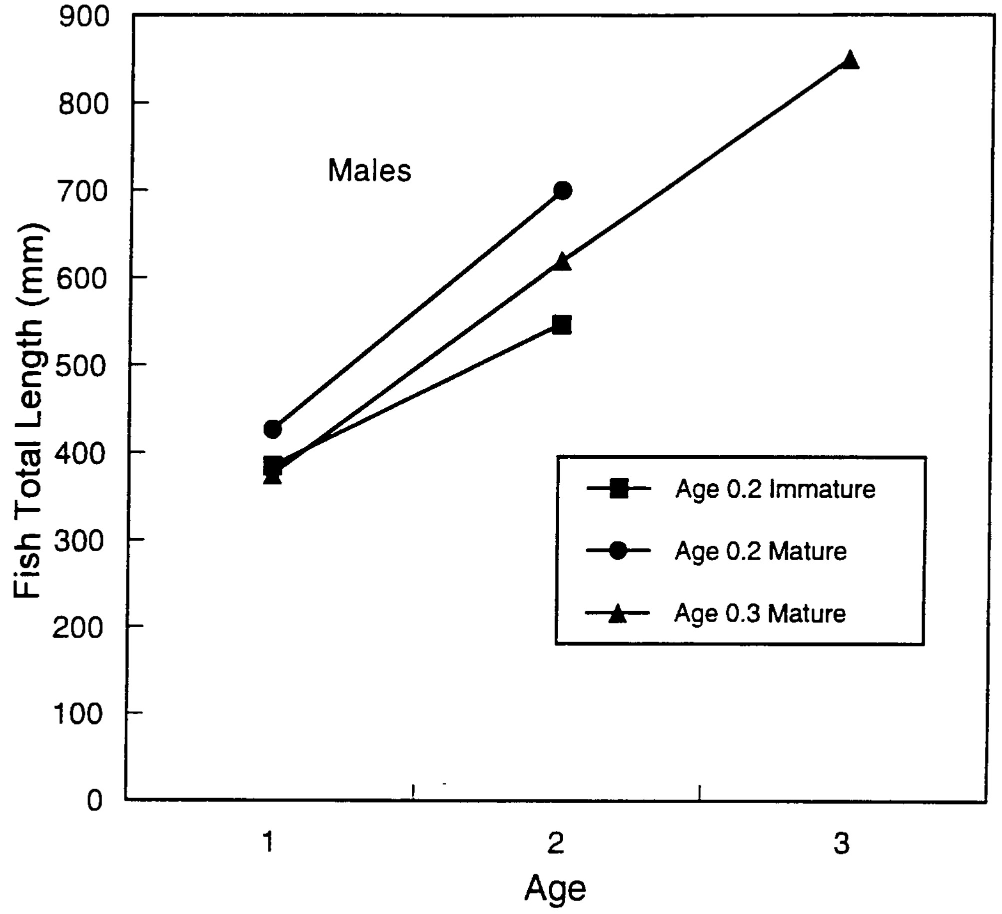

Figure 14. Lake Michigan chinook salmon back calculated annual growth increments for males based on total lengths of pooled sport and gill net harvested fish, 1994.

et al. 1990, Trippel 1993) and other fishes (Pitt 1975, Hay et al. 1988, Hartman and Margraf 1992, Houthuijzen et al. 1993). Jobling and Baarduik (1991) and Jobling et al. (1993) found that mature males grew faster than immature male and female Arctic charr *Salvelinus alpinus*. Sexual dimorphism in size is common in some fishes (Casselman 1987). Male steelhead trout *O. mykiss* grow faster than females in saltwater (Parker and Larkin 1959). Most of the difference in size between sexes in salmonids seems to be based on maturity, where faster growing fish mature earlier. In my analysis, I compared chinook salmon based on sex and maturity and found no differences in size between sexes. Parker and Larkin (1959) may have had different results if they had analyzed growth based on sex and maturity rather than just sex.

Factors other than growth may also influence age at maturity. Quinn and Unwin (1993) indicate that selection (artificial or natural) against older fish could be a mechanism regulating age at maturity. With the presence of BKD in Lake Michigan, I believe that there is a selection against older fish which could reduce the age at maturity. In Atlantic salmon, Riddell (1986) found that the fishery reduced age at maturity by genetically selecting against older fish. With a large heritable component in age at maturity for chinook salmon (Hard et al. 1985), hatchery practices could also have an effect on size and age at maturity in Lake Michigan. It is not evident that age at maturity has changed due to size selection from BKD or hatchery practices.

With low population levels of age 0.3 and 0.4 chinook salmon in Lake Michigan, the combination of age and growth data from sport and gill net harvested fish may be important to increase sample sizes. My data suggest that there are no differences between the two methods based on age, gender, and maturity specific mean total lengths. Anglers seem to catch the same size fish as gill nets, contrary to the findings of Miranda et al. (1987) with largemouth bass. A larger sample size of age 0.3 and 0.4 chinook salmon would increase confidence in these results. These data support the use of pooling sport caught and gill netted chinook salmon for growth analyses. However, it would be inappropriate to pool angler and gill net harvested chinook salmon unless samples are stratified by maturity, gender, and age.

There were, however, slight differences in the slopes and intercepts (*a*) of length to scale radii relationships between the sport and gill netted harvested fish. Carlander (1982) suggested that most variation in *a* is not due to population differences but is due to measuring scales at different angles, collecting scales from different areas of the body, season of collection, and samples with poor representation of small sizes. The angles of measurement and the season of collection were the same for both data sets in this study. There may be differences in scale sampling areas on the body between the two data sets. I collected the sport caught scales and MDNR employees collected the gill netted scales. There was also a lack of fish under 25.4 cm (10.0 in.) since this is the legal size limit for angled chinook salmon in Lake Michigan, and since mesh sizes for gill nets were too large to catch a representative sample of small fish.

Some reverse Lee's phenomenon appeared to be occurring with back calculated lengths from the pooled data in Table 13; age 0.1 lengths back calculated from older aged (age 0.2, 0.3, or 0.4) chinook salmon are larger than back calculated lengths of chinook salmon harvested at age 0.1. Tesch (1968) gave a good description and literature review of Lee's phenomenon. Reverse Lee's phenomenon occurs when back calculated lengths at a given age are larger than observed lengths at that age. Neilson and Geen (1986) also found reverse Lee's phenomenon when back calculating lengths of chinook salmon using otoliths. Some causes of reverse Lee's phenomenon could be selective natural mortality (greater survival of larger fish), selective fishing mortality, or non random sampling of the population (sampling the larger representatives). Some of these causes could occur in Lake Michigan. Larger chinook could be more vulnerable to the sport fishery; however, I found no difference in size between angler and gill net harvested chinook salmon in Lake Michigan. BKD may be selecting against slow growing or small fish, increasing the number of larger fish surviving to an older age. The low numbers of age 0.4 chinook salmon in the present Lake Michigan population could be due to low survival of small fish due to BKD.

The differences in growth of chinook salmon based on gender and maturity will be important to consider in future studies involving growth. Predator prey models developed for salmonids from Lake Michigan could be improved by considering these different growth trajectories. It will also be useful to management to monitor ages at maturity to see if changes occur with size selection from BKD and current hatchery practices. Evidence from the reverse Lee's phenomenon suggests that smaller hence slower growing fish are more vulnerable to BKD than faster growing fish. The critical period may be associated with the growth achieved by the first year of life; therefore, more research is needed to examine the early life history of chinook salmon in Lake Michigan. This research may reveal limiting factors on the growth of juvenile and yearling fish.

CHAPTER FOUR

Comparison of Size at Age for Chinook Salmon in Lake Michigan, 1983-1993

Introduction

A quantitative comparison of historical and current growth of chinook salmon may give some insights to their recent decline in Lake Michigan (Chapter One). A decrease in growth could be associated with declining alewife numbers, and it may indicate stress due to forage decline as the mechanism causing the outbreak of BKD. If there was no change in growth, perhaps another hypotheses for the outbreak of BKD would be more logical. Estimation of historic growth rates would also be beneficial to calibrate existing and future predator prey models for Lake Michigan salmonids (Stewart et al. 1981, Stewart and Ibarra 1991).

The ability to accurately age lake harvested chinook salmon using scales allows the estimation of age specific growth with confidence. Historic size data and scales can be analyzed to determine size at age using back calculation methods described in Chapter Three. The longest data set including scales from lake harvested fish is from the MDNR creel survey for Lake Michigan which began in 1983 (Rakoczy and Svoboda 1994). MDNR weir data are also available, but scales can not be aged accurately because of erosion which may lead to error in growth rates. Vertebrae have not been collected as weir data, even though vertebrae are the best calcified structures to use for aging mature chinook salmon (Hesse 1994).

The objectives of this chapter are to determine historic age and growth of chinook salmon by back calculation and compare past and present growth rates in

Lake Michigan. Another objective is to compare growth based on location of harvest. Traditionally, the sport fishery for chinook salmon in Lake Michigan begins in early spring in the southern part of the lake, and as the year progresses, the fishery moves north (Rakoczy and Svoboda 1994). Assuming that this movement in the fishery represents a seasonal movement in fish, then a large number of chinook salmon overwinter or at least spend early spring in the southern part of the lake. A growth comparison for chinook salmon harvested in the spring may give some understanding to why this migration occurs. If the migration of chinook salmon is following a migration of forage fishes, then spring harvested chinook salmon should show better growth in the south than in the north. Warmer water temperatures in the south may also improve chinook salmon growth.

Methods

Biological data were taken from samples collected by MDNR creel clerks between New Buffalo and Charlevoix. Clerks sampled anglers from the Michigan waters of Lake Michigan during open water season between 1 April and 31 March using stratified random sampling (Rakoczy 1992). Biological were taken on a percentage of fish sampled in the field at each port. These data consisted of total length (to 1 mm), weight (to 1 g), and scales. On occasion, observations of sex and maturity were also recorded. Creel clerks were trained each year to take scales from between the dorsal and adipose fin and above the lateral line.

Scales were pressed and aged using techniques described in Chapter Two. Scales exhibiting erosion were not used for analyses. An average of three measurements on scales from each fish were made on a Java Projection Computer System (Acker and Mitchell 1988) to determine back calculated lengths using the Fraser-Lee Method (see Chapter Three for details). Scale increments and fish lengths were input in the DISBCAL computer package (Frie 1982) for back calculation. A common intercept of 86 mm was used for all years (Carlander 1982, Chapter Three).

Samples from each port were combined into one Lake Michigan sample for each year to compare growth. Mean back calculated lengths at each age were compared for each year. Lengths were calculated back to the time of annulus formation, which occurs between June and July, for that current year and age of fish only. For example, mean length of age 0.2 fish in 1983 represents total lengths back calculated to the 2nd annulus of age 0.2 fish harvested in 1983; it was not back calculated total length to the 2nd annulus of age 0.3 or 0.4 fish harvested in 1984 or 1985. Only age 0.1 through 0.4 chinook salmon were analyzed. Age 0.5 fish and any chinook salmon that appeared to have one year of stream residency were not used because those life history types have not been validated using scale methods.

Length of an individual fish rarely decreases with time; however, weight may increase or decrease for any given length of an individual fish (Wootton 1990). These changes in weight may indicate more subtle changes in growth relative to length. Therefore, the Fulton Index of condition was also compared because condition is more sensitive to subtle changes in growth. The Fulton Index was recommended for fish showing isometric growth ($W=aL^3$) where weight is symmetric with length by a factor of three (Tesch 1968, Anderson and Gutreuter 1983). Chinook salmon from

Lake Michigan have this isometric growth with a slope of 3.08 based on data from 1983 to 1993 (see Table 17). The Fulton Index (*FI*) of condition was calculated using the following equation (Anderson and Gutreuter 1983):

$$FI = \frac{W}{L^3} X$$

where *W* is weight (g), *L* is length (mm), and *X* (100,000) is an arbitrary scaling constant. Back calculated length of each individual fish was used to compute individual weight. Weights were then estimated from weight-length relationships calculated from fish harvested before 30 June for each year. Therefore, lengths, weights, and condition were based on spring measurements.

Mean back calculated lengths and Fulton Indices were also used to compare growth between chinook harvested in the north and south sections of Lake Michigan before 30 June. Chinook harvested from Muskegon and to the south were pooled to form the south section, while the north section consisted of all ports from Ludington north. To increase sample size, 1985 and 1986 samples were combined. These years were before the onset of BKD.

Total length was back calculated only to spring for each age of fish; henceforth, this variable will be called back calculated length. Back calculated lengths and Fulton Indices were compared for fish sampled from 1983 through 1993. Assumptions of normality and equal variances were tested using coefficients of skewness, kurtosis, and F-tests for equal variance (Norusis 1993). Age 0.1 and 0.2

chinook salmon had unequal variances in mean back calculated lengths, so nonparametric Kruskal-Wallis and Mann-Whitney U tests were used to determine differences among and between years. Mean back calculated lengths of age 0.3 and 0.4 fish were compared with ANOVA's, and multiple comparisons were made using Bonferroni's test. All ages had unequal variances with Fulton Index data so Kruskal-Wallis and Mann-Whitney U tests for equal means were used. With the comparison of back calculated lengths and Fulton Indices for fish from the north and south, F-tests for equality of means were used for normally distributed data with equal variances and Kruskal-Wallis and Mann-Whitney U tests of equal means were used otherwise. All tests were performed at the 5 % level of significance using SPSS (Norusis 1993).

Results

Most chinook salmon in the sample were harvested from Grand Haven south and from Manistee north. A total of 2,647 scales were aged and measured for samples from 1983 through 1993. The proportion of the samples comprising each age class decreased for ages 0.3 and 0.4 fish and increased for age 0.1 fish from 1983 to 1993 (Table 14). The average age of salmon in the sample also decreased from a high of 2.59 years in 1986 to 1.53 in 1993. The number of chinook exhibiting stream annuli was variable among years and comprised a low percent of total catch (Table 15). Age 0.5 chinook salmon were only observed in 1987 with a total of three.

Mean back calculated length at age 0.1 significantly increased from 1986 to 1988 and then decreased from 1988 to 1993 (Table 16; Figure 15; Mann-Whitney U; $p<0.05$). For age 0.2 fish, mean back calculated length increased significantly from

Table 14. Proportion of the sample comprising each age class, and average age for chinook salmon from Lake Michigan (1983-1993). Sample sizes in parentheses.

Year	Proportion At Age 0.1	0.2	0.3	0.4	Average Age
1983	0.19 (34)	0.40 (73)	0.36 (66)	0.05 (10)	2.28 (183)
1984	0.22 (46)	0.41 (85)	0.30 (63)	0.07 (14)	2.22 (208)
1985	0.16 (36)	0.38 (88)	0.36 (82)	0.10 (23)	2.39 (229)
1986	0.07 (25)	0.33 (118)	0.53 (189)	0.08 (27)	2.59 (359)
1987	0.15 (69)	0.34 (162)	0.35 (164)	0.16 (76)	2.52 (471)
1988	0.18 (67)	0.29 (106)	0.41 (149)	0.11 (41)	2.45 (363)
1989	0.23 (42)	0.44 (82)	0.26 (48)	0.08 (14)	2.18 (186)
1990	0.30 (41)	0.51 (70)	0.16 (22)	0.03 (4)	1.92 (137)
1991	0.53 (73)	0.33 (45)	0.12 (17)	0.01 (2)	1.62 (137)
1992	0.47 (115)	0.30 (74)	0.19 (46)	0.03 (8)	1.76 (243)
1993	0.56 (74)	0.31 (41)	0.11 (14)	0.02 (2)	1.53 (131)

Table 15. Percent of sample with one year of stream residence, or of age 0.5 fish, based on the total sample of chinook salmon each year (1983-1993). Sample sizes in parentheses.

Year	Sample Size	Age Type 1.0	1.1	1.2	1.3	0.5
1983	183					
1984	212		1.89 (4)			
1985	230		0.43 (1)			
1986	361	0.28 (1)	0.28 (1)			
1987	479		0.63 (3)		0.42 (2)	0.63 (3)
1988	375		0.80 (3)	1.07 (4)		
1989	186					
1990	140		0.71 (1)	0.71 (1)	0.71 (1)	
1991	142	0.70 (1)	2.87 (4)			
1992	257	1.56 (4)	3.89 (10)			
1993	132		0.76 (1)			

Table 16. Mean back calculated length at age for chinook salmon taken by anglers in Lake Michigan from 1983 to 1993 (sample sizes in parentheses).

	Mean Length at Age			
Year	0.1	0.2	0.3	0.4
1983	395.6 (34)	609.1 (73)	807.8 (66)	833.5 (10)
1984	385.0 (46)	620.0 (85)	764.9 (63)	891.8 (14)
1985	389.3 (36)	620.5 (88)	785.7 (82)	859.8 (23)
1986	372.7 (25)	632.8 (118)	790.7 (189)	853.1 (27)
1987	398.7 (69)	641.1 (162)	822.8 (164)	870.4 (76)
1988	416.5 (67)	662.1 (106)	843.8 (149)	915.4 (41)
1989	400.0 (42)	638.2 (82)	815.1 (48)	881.6 (14)
1990	389.6 (41)	613.9 (70)	814.4 (22)	871.1 (4)
1991	398.4 (73)	615.5 (45)	819.7 (17)	815.4 (2)
1992	380.3 (115)	658.9 (74)	853.4 (46)	919.3 (8)
1993	370.4 (74)	615.2 (41)	891.1 (14)	1047.4 (2)

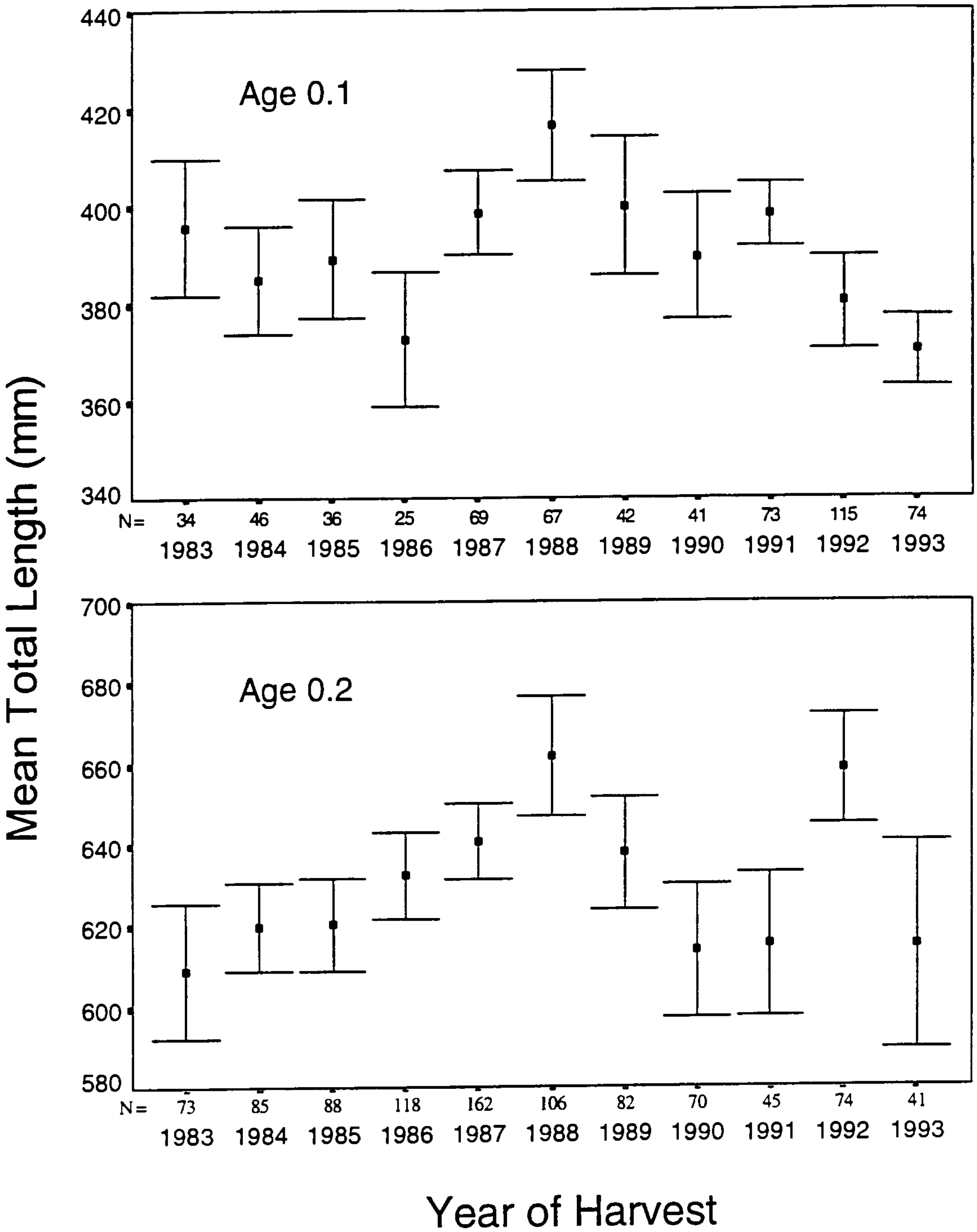

Figure 15. Back calculated lengths of age 0.1 and 0.2 chinook salmon from Lake Michigan, 1983-1993. Means are represented by filled squares, brackets represent 95% confidence intervals. Sample size is below the x axis.

1983 to 1988, decreased from 1988 to 1990, increased from 1991 to 1992, and then decreased from 1992 to 1993 (Figure 15; Mann-Whitney U; $p<0.05$).

Age 0.3 and 0.4 chinook salmon displayed significant annual differences in back calculated length as well (ANOVA, $p<0.05$). Age 0.3 fish had a significant decrease in back calculated length from 1983 to 1984 and an increase from 1984 to 1993 (Figure 16; Bonferroni Multiple Comparisons, $p<0.05$). Mean back calculated length for age 0.4 fish increased from 1987 to 1988 and decreased in 1991 despite the low sample size (Figure 16; Bonferroni Multiple Comparisons, $p<0.05$).

Weight-length relationships were calculated for chinook salmon harvested in spring (Table 17). Mean slope of the weight-length relationships before BKD (1983-1987) was significantly lower (t-test, $p<0.001$) than the mean slope after BKD (1988-1993) with values of 2.9891 and 3.2179, respectively. Predicted weights at age for Lake Michigan chinook salmon are listed in Table 18. These weights have recent decreasing trends for ages 0.1 and 0.2 from 1988 to 1993 (Mann-Whitney U, $p<0.001$) with an increase in 1992 for age 0.2 (Mann-Whitney U, $p<0.001$). Age 0.3 significantly increased in weight from 1987 to 1993 (Mann-Whitney U, $p=0.001$), and age 0.4 significantly increased in weight between 1987 and 1992 (Mann-Whitney U, $p=0.003$).

Age 0.1 and 0.2 fish exhibited significant differences in Fulton Index among years (Table 19; Kruskal-Wallis, $p<0.05$) but had no consistent trends between 1983 and 1993 (Figure 17). There was a significant increase in Fulton Index in 1992 for both ages, but mean condition decreased again in 1993 (Mann-Whitney U, $p<0.05$).

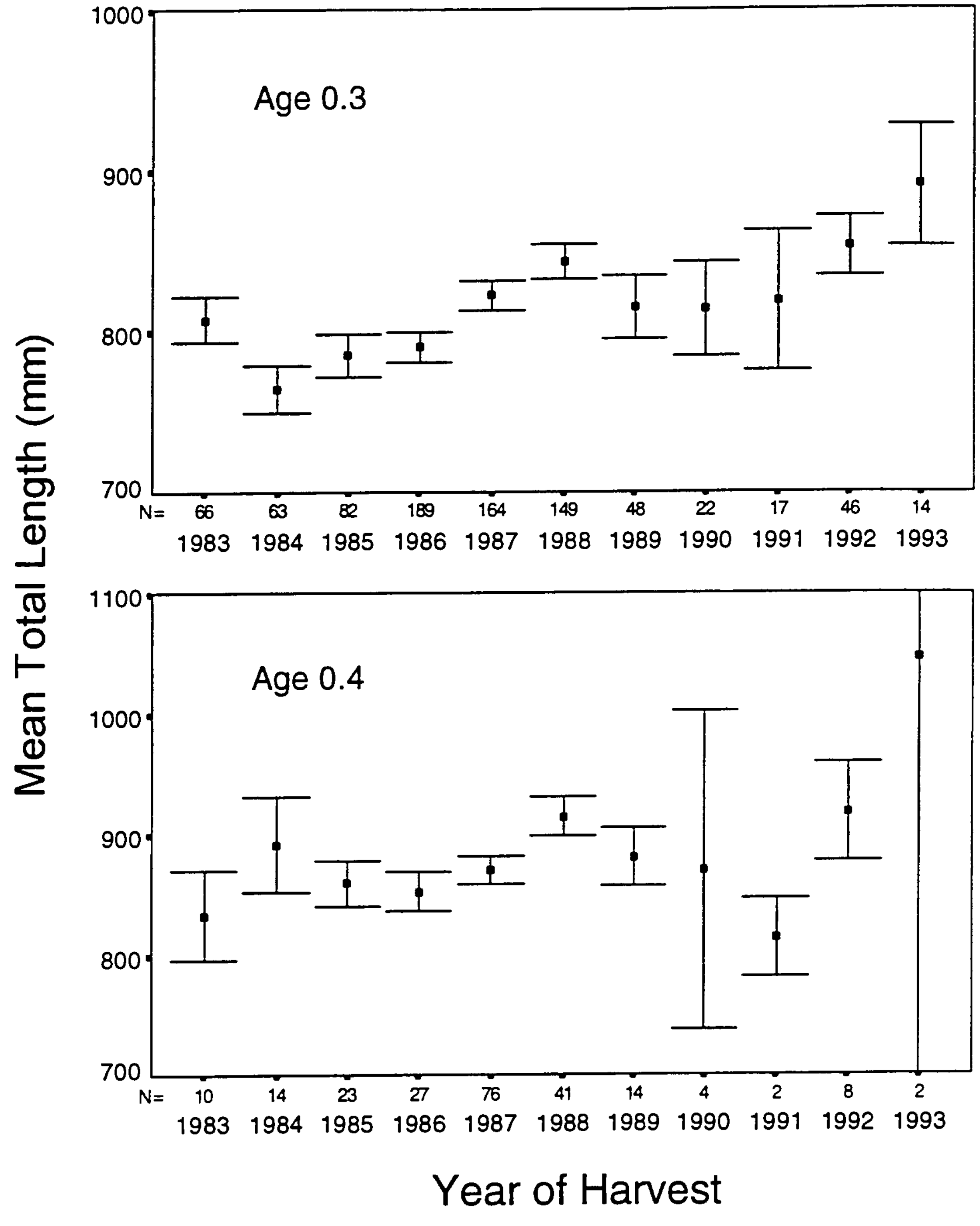

Figure 16. Back calculated lengths of age 0.3 and 0.4 chinook salmon from Lake Michigan, 1983-1993. Means are represented by filled squares, brackets represent 95% confidence intervals. Sample size is below the x axis.

Table 17. Weight (g)-Length (mm) relationships for chinook salmon harvested by anglers from Michigan waters of Lake Michigan, 1983-1993. Harvest dates were between 1 April and 30 June. Evaluations were fit to Log W = Log a + b Log L.

Year	Y-Intercept (Log a)	Slope (b)	Sample Size
1983	-5.26094	3.09604	182
1984	-4.84672	2.94476	208
1985	-4.73427	2.90916	227
1986	-5.25698	3.08528	360
1987	-4.72522	2.91032	469
1988	-5.38796	3.12924	362
1989	-5.92376	3.33464	186
1990	-5.54403	3.19663	136
1991	-5.70161	3.25543	130
1992	-5.27383	3.10675	246
1993	-5.79292	3.28479	135
AVG.	-5.23682	3.08483	2642

Table 18. Mean back calculated weight (g) for each age of chinook salmon from Lake Michigan, 1983 to 1993.

	Mean Weight at Age			
Year	0.1	0.2	0.3	0.4
1983	584.7	2260.7	5274.3	5784.2
1984	565.9	2408.6	4567.1	7298.3
1985	613.5	2474.9	4997.7	6462.7
1986	469.8	2517.4	5055.0	6347.5
1987	659.0	2798.8	5919.0	6975.7
1988	725.6	3149.9	6615.1	8486.4
1989	562.0	2678.9	6034.0	7723.0
1990	537.2	2364.6	5784.7	7214.4
1991	592.6	2471.5	6278.5	5960.3
1992	680.2	3300.9	6986.8	8627.7
1993	428.1	2311.0	7380.8	12640.7

Table 19. Mean Fulton Indices for each age of chinook salmon from Lake Michigan, 1983 to 1993.

	Mean Fulton Index at Age			
Year	0.1	0.2	0.3	0.4
1983	0.91	0.96	0.98	0.99
1984	0.96	0.99	1.00	1.01
1985	1.01	1.01	1.01	1.01
1986	0.88	0.96	1.00	1.01
1987	1.01	1.03	1.04	1.05
1988	0.96	1.03	1.07	1.09
1989	0.83	0.99	1.08	1.12
1990	0.87	0.98	1.04	1.06
1991	0.92	1.02	1.10	1.10
1992	1.18	1.13	1.10	1.10
1993	0.82	0.93	1.02	1.07

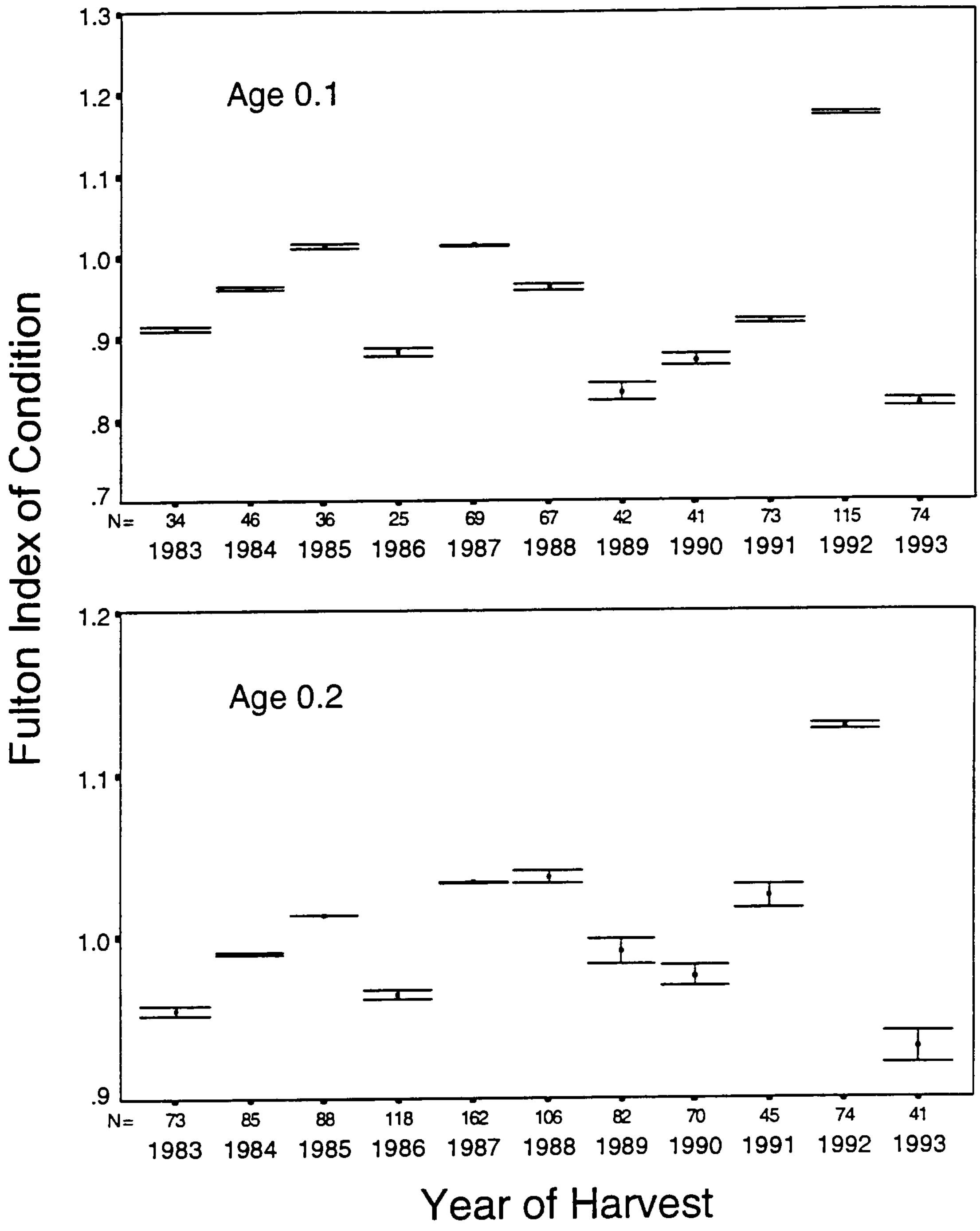

Figure 17. Fulton Indices of age 0.1 and 0.2 chinook salmon from Lake Michigan, 1983-1993. Means are represented by filled squares, brackets represent 95% confidence intervals. Sample size is below the x axis.

Age 0.3 and 0.4 condition also differed significantly among years (Kruskal-Wallis, $p<0.05$). There was an increasing trend in condition for age 0.3 and 0.4 between1983 and 1993 (Figure 18). Mean Fulton Index increased by 0.062 for age 0.3 and 0.076 for age 0.4 after the onset of BKD based on the difference between the average Fulton Index before and after 1988 for each age.

Age 0.1 chinook salmon achieved greater lengths (Table 20; F-test, $p=0.02$) in the southern region of Lake Michigan than in the northern region. There were no significant differences between regions for ages 0.2, 0.3, or 0.4 (F-test, $p<0.05$). Condition was significantly greater in the southern region for age 0.1 (F-test, $p<0.001$), age 0.2 (Kruskal-Wallis, $p<0.001$), and age 0.3 (Kruskal-Wallis, $p<0.001$). There was no significant difference in condition between the two regions for age 0.4 chinook salmon (F-test).

Discussion

Age 0.1 chinook salmon in Lake Michigan have decreased in growth between 1988 and 1993, while age 0.3 and 0.4 chinook salmon have increased in growth. The increase in growth of ages 0.3 and 0.4 after BKD suggests that there was high competition for food prior to BKD. Slow growth prior to BKD agrees with Hansen's (1986) observation of a decrease in condition of chinook between 1969 and 1984 which he attributed to forage limitation. Bioenergetic models also predicted declines of chinook salmon growth in Lake Michigan because of the reduction in adult alewife biomass (Stewart et al. 1981, Stewart and Ibarra 1991).

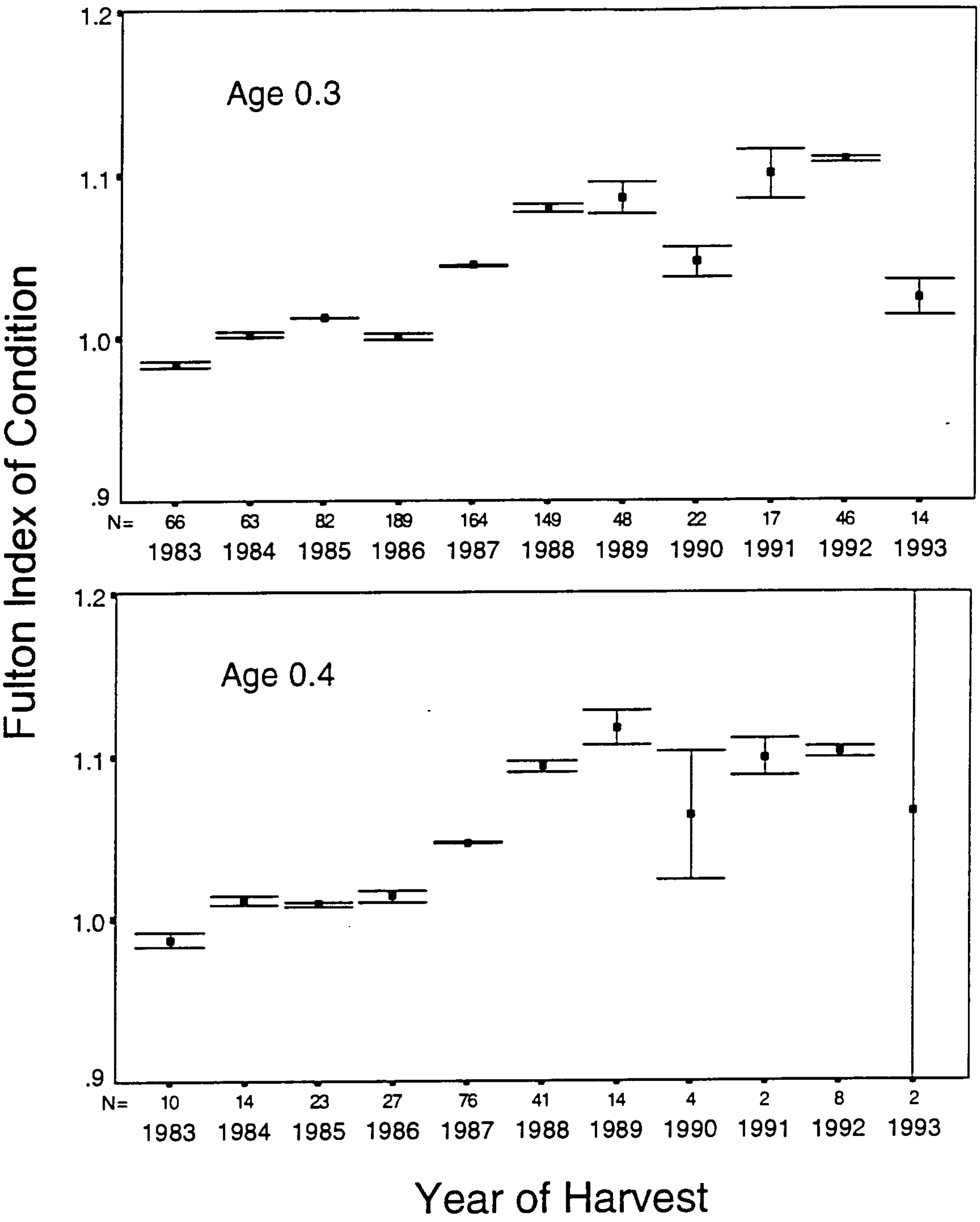

Figure 18. Fulton Indices of age 0.3 and 0.4 chinook salmon from Lake Michigan, 1983-1993. Means are represented by filled squares, brackets represent 95% confidence intervals. Sample size is below the x axis.

Table 20. Comparison of mean back calculated length (mm) and Fulton Indices (FI) for chinook salmon harvested in the northern (Ludington and north) and southern (Muskegon and south) regions of Lake Michigan before 30 June.

	North			South		
Age	Length	FI	Sample Size	Length	FI	Sample Size
0.1	343.23	0.87	2	409.00	1.02	4
0.2	628.44	0.96	64	627.83	1.01	45
0.3	797.91	1.00	111	788.65	1.01	53
0.4	852.37	1.01	7	862.41	1.01	15

The increase in back calculated length and condition of age 0.3 and 0.4 chinook salmon after BKD may be associated with an intra-specific competitive release, where by BKD caused significant mortality and reduced the density of older fish. With less competition for prey, age 0.3 and 0.4 chinook probably experienced increased growth rates, which is supported by the increases in mean length and condition. Density-dependent growth has been documented for kokanee salmon *O. nerka* (nonanadromous form) in Idaho reservoirs (Rieman and Myers 1992) and sockeye salmon *O. nerka* in Bristol Bay (Rogers 1980). Increased growth and production as a response to reduced competition is well documented for fishes in the genus *Perca* (Schneider and Crowe 1980, Hanson and Legget 1985, Persson 1986, Hayes et al. 1992). The increase in growth may be compounded or explaind by the possibility that fast growing fish survived BKD more often than slow growing fish, increasing the frequency of these rapid growing fish in the population. Although differential mortality based on size may be an alternative to the increase in growth from competitive release, these hypotheses are not mutually exclusive.

Mean back calculated total length and condition decreased for age 0.1 chinook after BKD. This decline may have been due to a shift in fishing techniques to smaller lure sizes (from plugs to spoons) allowing for more small chinook to be harvested, it could also be due to a decline in forage abundance, or an increase in abundance of age 0.1 chinook salmon due to additional stocking and natural reproduction. Stocking of chinook salmon by Michigan increased 23% between 1987 and 1993, but overall stocking of chinook by all jurisdictions decreased by 30%

between 1989 and 1993 (Holey 1995). There were no major trends in age 0.2 lengths and condition. Significant increases in condition for age 0.1 and age 0.2 fish in 1992 may be correlated to the warm spring that year (NOAA 1992).

The decrease in growth of age 0.1 may represent a critical period. If a chinook salmon can achieve good growth through its first year, it may be able to survive BKD, and then either live to an older age or mature at an earlier age. The abundance of young-of-the-year and small alewife as forage and the abundance of young chinook salmon may be affecting the growth of age 0.1 chinook salmon, but the key may be the growth achieved between smoltification and age 0.1. In that case, abundance of plankton and terrestrial invertebrates may be more important than alewife. With recent invasions of *Bythotrephes cederstroemii*, a predatory zooplankter (Lehman 1987), and zebra mussels *Dreissena polymorpha*, planktonic invertebrates may have changed in species composition and numbers affecting both young-of-the-year alewife and chinook salmon.

The last indication that there was a change in growth is the difference in slope before and after the onset of BKD. A larger slope indicates an increase in condition or more weight per given length. The mean slope before BKD was lower than the mean slope after BKD. This suggests that condition, hence growth, was better after 1988 for the population. These slopes were based on spring lengths and weights so there may be some variation between years due to temperature and other physical factors. This index of growth also combined all ages so differences in growth by age could not be determined.

The MDNR Creel Survey data also had several interesting age trends for chinook salmon. The first was a decrease in the average age in the catch, where the proportion of age 0.1 chinook increased and the proportion of age 0.3 and 0.4 chinook decreased from 1983-1993. The decrease in the proportion of age 0.3 and 0.4 chinook was undoubtedly due to high mortality from BKD. The increase in number of age 0.1 chinook was probably due to the increase in stocking or natural reproduction of chinook salmon in the Michigan waters of Lake Michigan. It may also be due to the shift to smaller lure sizes by fishers and a shift to fishing over deeper water where one-year-old chinook tend to inhabit (Elliott 1994). Perhaps the appetite of the younger chinook also increased, making them more inclined to strike a lure. Beukema (1968) found that starved threespine sticklebacks directed more feeding attempts at inedible objects. The combination of using smaller lure sizes and the increased attacks on lures due to hunger may have increased susceptibility of younger chinook to the sport fishery.

The number of alternative age chinook salmon contributing to the sport fishery varied from year to year. Fish spending one year in the stream contributed a range of 0.0 % to 3.89 %. The greatest percent of stream yearlings was in 1992 which was a warm spring (NOAA 1992). A decrease in growth of smolts will increase the number staying in the stream another year (Parker and Larkin 1959). Therefore, the number of stream yearlings may be dependent on late winter and spring physical conditions. This would explain the variability from year to year. Age 0.5 chinook were only observed in 1987 at 0.63 %. Since age at maturity is dependent on growth (Parker and Larkin 1959, Healey 1986, Riddell 1986, Neilson and Geen 1986), this may indicate that growth was below normal because more fish delayed reproduction (Mangel 1994). More age 0.4 and 0.5 chinook salmon contribute to the sport fishery in Lake Superior (Berg 1978, Peck 1992) where low temperature and production result in slower growth hence later age at maturity. However, age 0.5 fish may also indicate better survival to reach older age. In any event, alternative ages of chinook salmon contributed a low percentage to the total Lake Michigan sport fishery.

Not only were there differences in age and growth between years, but there were also differences in growth within years related to spring harvest location. Assuming that chinook salmon harvested in a region of Lake Michigan before 30 June resided in that region for the entire spring, then spring growth was better in the southern compared to the northern part for younger fishes. Conditions of ages 0.1, 0.2 and 0.3 were also higher in chinook salmon harvested in the south compared to the north. However, mean back calculated lengths were greater in the north for ages 0.2 and 0.3, and condition was greater in the north for age 0.4. The increase in spring growth of chinook salmon in the south suggests that earlier warming of the water may concentrate forage in that region, and that chinook salmon may benefit in the southern region of the lake by foraging earlier in the spring. Larval fish may also become available earlier for age 0.1 chinook salmon. However, the power of these data was limited because there was a low sample size of age 0.1, and two years of data were combined. Further support for increased growth benefits in southern Lake Michigan would be the movement of the chinook sport fishery from south to north as the summer progresses (Rakoczy and Svoboda 1994). Some of this northern migration may be the return of mature salmon to their natal streams, and it may also be the following of forage (Sommers et al. 1981). Increasing temperatures and lake currents (Ayers et al. 1958, Sato and Mortimer 1975) may also move forage and salmon north.

Was BKD caused by stress due to declines in forage abundance? There were significant declines in condition for age 0.1 and 0.2 chinook salmon in 1986, prior to the onset of BKD. This decrease in condition may indicate that stress caused the initiation of BKD, and the evidence for improved growth in age 0.3 and 0.4 chinook salmon after BKD indicates forage changes as the potential stress. Nonetheless, other hypotheses for the BKD outbreak can not be ruled out. Using infected eggs and sperm in hatcheries and stocking chinook at the same time sick fish are present in shallow waters should still be considered as alternative hypothesis for the BKD outbreak (Elliott 1994). A growth decline prior to the onset of BKD was also indicated by the high proportion of older ages in the sport fishery in 1987, which included the only year that 0.5-year-old fish were observed. Increased age at maturity could signify decreased growth of the population.

Recognition of the changes in age and growth of chinook are important. The reasons for the changes are difficult to answer due to the complexity of Lake Michigan and the several changes that have occurred within it. The growth compensation after BKD for age 0.3 and 0.4 and decreased condition of age 0.1 and 0.2 prior to BKD implicates that forage changes may have been limiting chinook salmon in Lake Michigan. Therefore, the decrease in stocking of chinook salmon into Lake Michigan is suggested to return historical growth rates and survival. Lower stocking levels may allow alewife numbers to rebound providing better forage for chinook salmon in the future and may restore the sport fishery for chinook salmon in Lake Michigan.

APPENDICES

APPENDIX A

Table 21. Mean scale increment length (mm) for age 0.1 (focus to 1st annulus), age 0.2 (1st to 2nd annulus), age 0.3 (2nd to 3rd annulus), and age 0.4 (3rd to 4th annulus) chinook salmon sport harvested from Lake Michigan, 1983-1993.

	Mean Scale Increment			
Year	Age 0.1	Age 0.2	Age 0.3	Age 0.4
1983	1.646	1.140	0.911	0.682
1984	1.572	1.221	0.950	0.651
1985	1.500	1.215	0.845	0.516
1986	1.596	1.264	0.821	0.510
1987	1.657	1.293	0.900	0.509
1988	1.620	1.295	0.838	0.523
1989	1.627	1.300	0.912	0.612
1990	1.670	1.284	1.027	0.628
1991	1.743	1.303	1.006	0.827
1992	1.563	1.368	0.985	0.570
1993	1.633	1.305	1.165	0.542

APPENDIX B

Table 22. Ford's growth equation ($L_{t+1} = L_\infty (1-k) + kL_t$) and Brody's coefficients ($K=-\ln k$) for sport harvested chinook salmon from Lake Michigan, 1983-1993.

Year	L_∞ (1-k)	*k*	K
1983	400.02	0.5769	0.5501
1984	377.96	0.6498	0.4311
1985	389.34	0.6117	0.4915
1986	385.29	0.6170	0.4828
1987	405.53	0.5963	0.5171
1988	417.19	0.6078	0.4979
1989	401.71	0.6088	0.4962
1990	391.03	0.6188	0.4800
1991	408.79	0.5523	0.5932
1992	395.92	0.6487	0.4328
1993	361.92	0.7864	0.2403

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