SPATIAL, TEMPORAL, AND COHORT-RELATED PATTERNS IN THE CONTRIBUTION OF WILD CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) TO TOTAL CHINOOK HARVEST IN LAKE MICHIGAN

By

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ABSTRACT

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During 2006–2010, the majority of hatchery-produced Chinook salmon (*Oncorhynchus tshawytscha*) stocked into Lake Michigan were marked with a combination of oxytetracycline (OTC), coded-wire-tags (CWT), and fin-clips to distinguish between hatchery and wild origin. The goals of this research were to: (1) evaluate the accuracy and reproducibility of the OTC mark, (2) examine spatial, temporal, and cohort-related patterns in the contribution of wild Chinook salmon, and (3) explore how differences in size-at-age and maturity-at-age may affect the proportion of wild Chinook salmon. OTC mark accuracy and reproducibility was determined to be adequate based on the error matrix fish, OTC mark quality distribution, and OTC mark presence/absence reader agreement was excellent. The lakewide proportion of wild age-1 Chinook salmon for four year-classes ranged from 53.52 to 56.92% with little interannual variation. The proportion of wild Chinook salmon increased as the fish became older (i.e., age-effect), suggesting differential survival between hatchery and wild fish. The proportion of wild age-1 Chinook salmon was greater in Michigan than Wisconsin, but was similar for older ages. The proportions of wild Chinook salmon for northern and southern Lake Michigan were similar for all four age-classes. The proportion of wild Chinook salmon in the northeast, northwest, and southwest regions all had an age-effect, however, the southeast region did not have an age-effect. The southeast region had the highest proportion of wild age-1 Chinook salmon.

This thesis is dedicated to my family, who began natural resource management in the early 1900s and showed me how to cherish the great outdoors.

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The opportunity to undertake my graduate school endeavor was provided by Dr. Michael Jones, who helped guide my development as a student, researcher, and professional. I would like to thank my committee members, Dr. Travis Brenden and Dr. Cheryl Murphy for their advice and insight that benefited my project. I am thankful for all of the assistance provided by the Department of Fisheries and Wildlife faculty and staff.

I am forever grateful to my lab mates, friends, and family; you make life great and work enjoyable. I have an indescribable gratitude for my wife, Elaina, for her support, love, and friendship during my graduate education and research.

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INTRODUCTION

Currently, Chinook salmon (*Oncorhynchus tshawytscha*) is one of the most important components of the Lake Michigan pelagic fish community and the recreational fishery. The lakewide stocking program for Chinook salmon and other salmonine species, started in the mid-1960s, and greatly altered the Lake Michigan fish community by substantially reducing the abundance of their major prey, alewife (*Alosa pseudoharengus*), creating a more balanced offshore predator-prey system (Tanner and Tody 2002; Hansen and Holey 2002; Madenjian et al. 2008). At the same time, this stocking program led to the establishment of a multi-billion dollar recreational fishery (Keller et al. 1990; Hansen and Holey 2002; Tanner and Tody 2002). Since the mid-1980s, stocking of salmonids was great enough to raise questions about the stability of the salmonine-alewife predator-prey system (Koonce and Jones 1994). More recently, evidence has accumulated that natural recruitment of Chinook salmon in Lake Michigan has reached levels that rival the additions of hatchery stocked fish each year (Hesse 1994; Jonas et al. 2008). Future management of this vitally important component of the fishery will therefore depend on a better understanding of the contribution of natural origin Chinook salmon to the lake and fishery, and the factors that may influence this contribution. The research described in this thesis evaluated a recently employed mass-marking method to assess natural origin Chinook salmon recruitment, and examined factors that influence variation in the proportion of natural Chinook salmon in space and time.

Early assessments of Lake Michigan Chinook salmon natural recruitment were achieved using mark-and-recapture techniques with hatchery stocked fish; either by stream-specific surveys or by partial lakewide oxytetracycline (OTC) surveys (Jonas et al. 2008; Figure 1). Stream-specific surveys were conducted by counting out-migrating wild smolts in tributaries that feed into Lake Michigan, whereas partial lakewide OTC surveys were accomplished by using lakewide OTC mass-marking techniques and collecting Chinook salmon tail samples from only certain areas of Lake Michigan. The most recent assessments of Lake Michigan Chinook salmon natural recruitment, which were the focus of this thesis, also relied on OTC mass-marking, but with a comprehensive, lakewide evaluation plan.

OTC is an antibiotic that has been effectively used to mark fish bony structures (e.g., otoliths and vertebrae). Hatchery-reared fish can be successfully marked and distinguished from natural origin populations with OTC mass-marking by a variety of techniques including immersion, injection, and feed (Rutherford et al. 2002). Lake Michigan fishery agencies chose to mass-mark Chinook salmon via OTC laced food because it is considered less expensive then alternative marking methods, but still results in a reliable and detectable mark that is indicative of a hatchery source (Hesse 1994; Rutherford et al. 2002; Johnson et al. 2010). When young salmon are administered OTC feed while in a hatchery, it produces a long-lasting mark in salmon vertebrae, which can be detected with a microscope equipped with a black light (Swartz 1971; Trojnar 1973; Rutherford et al. 2002; Johnson et al. 2010).

In Lake Michigan from 1979 to 2004, five investigations have provided evidence that naturally-produced Chinook salmon smolt abundance increased steadily since their introduction in 1967, from an early estimate of 600,000 smolts to a peak abundance of nearly 7 million smolts in 2001 (Jonas et al. 2008; Claramunt et al. 2012; Figure 1). In

1979, Carl (1982) estimated Chinook salmon natural reproduction from Lake Michigan tributaries at 600,000 fish per year using stream-specific surveys (Figure 1). In 1983, Keller et al. (1990) estimated Chinook salmon natural reproduction at 1.5 million fish per year, also by stream-specific surveys (Figure 1). In the early 1990s, two OTC studies estimated Chinook salmon natural reproduction ranged between 1.6 and 3.8 million fish per year (Hesse 1994; Jonas et al. 2008; Figure 1). In the early 2000s, another OTC study estimated Chinook salmon natural reproduction ranged between 2.5 and 6.8 million fish per year (Jonas et al. 2008; Claramunt et al. 2012; Figure 1). These studies suggest that Lake Michigan Chinook salmon natural reproduction increased steadily from the 1980s to the early 2000s, and can vary from three- to four-fold annually (Claramunt et al. 2012). By the early 2000s, OTC estimates indicated that wild Chinook salmon accounted for as much as 50% of the lake population (Claramunt et al. 2012).

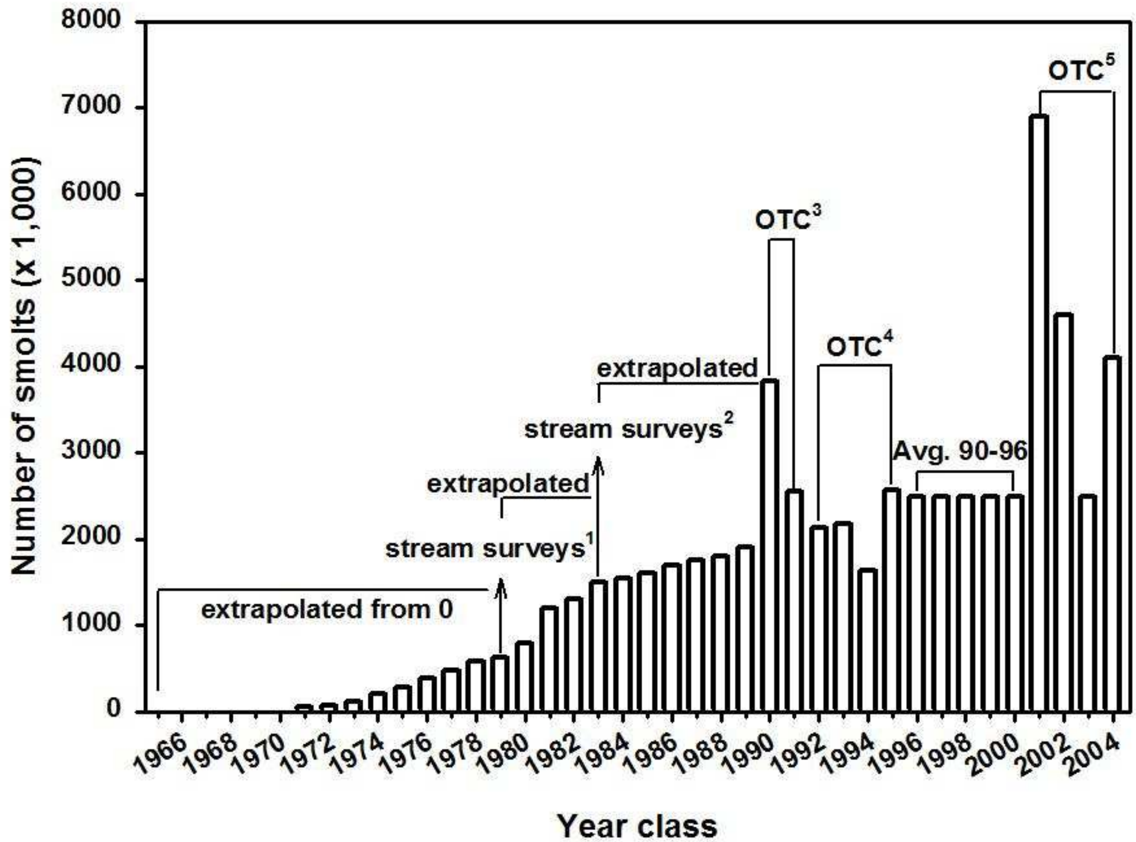

Figure 1.—Estimates of natural Chinook salmon smolt reproduction from Lake Michigan tributaries, 1965-2004. OTC refers to the recapture of adults marked as fingerlings with oxytetracycline ([1]Carl 1982; [2]Keller et al. 1990; [3]Hesse 1994; [4]E.S. Rutherford and D.F. Clapp, unpublished data; [5]R.M. Claramunt and J. Johnson (Michigan Department of Natural Resources), unpublished data; Jonas et al. 2008).

The earlier, stream-specific assessments of wild Chinook salmon recruitment were based on methods that required strong assumptions to extrapolate the sample data to a lakewide reproduction estimate. Mass-marking hatchery fish using OTC or some other unique mark offers the great advantage that the entire stocked cohort can be marked and identified, avoiding the need for extrapolation, and allows managers to determine the lakewide contribution of natural and hatchery origin Chinook salmon in Lake Michigan. Additionally, these earlier attempts to estimate Chinook salmon natural reproduction in Lake Michigan using OTC mass-marking encountered other problems including: (1) inconsistent marking procedures in the hatcheries, (2) lack of consistency in quality assurance quality control (QAQC) samples collected at the hatcheries, and (3) lack of a lakewide coordinated sampling plan (Szalai and Bence 2002; Rutherford et al. 2002).

Lake Michigan fishery managers recognized the need for a better understanding of natural Chinook salmon reproduction, particularly for estimating overall demand for prey consumption by the Lake Michigan Chinook salmon population as an input to establishing sustainable stocking rates. Therefore, in March 2006, the Lake Michigan Committee (LMC) charged the Salmonid Working Group (SWG) to provide a suite of options to evaluate the contributions of hatchery and natural origin Chinook salmon in Lake Michigan. In response the SWG developed and presented a series of recommendations to establish a long-term, coordinated, and collaborative lakewide OTC mass-marking program to evaluate Lake Michigan Chinook salmon natural reproduction (Claramunt et al. 2006; R. Claramunt, Michigan DNR, personal communication).

In 2006 the SWG and LMC reached an agreement on the methodology necessary for successful implementation of the lakewide Chinook salmon OTC mass-marking program. This program and research study is unique and significant because it is the first known attempt to evaluate the lakewide contribution of natural and hatchery origin Chinook salmon for Lake Michigan. The program also included strong buy-in across Lake Michigan agencies for mark and evaluation procedures and better methods for quantifying error rates. In 2006 all of the agencies responsible for stocking Chinook salmon into Lake Michigan (i.e., Illinois Department of Natural Resources (IDNR), Indiana Department of Natural Resources (IDNR), Wisconsin Department of Natural Resources (WDNR), and MDNR), began a five year lakewide OTC mass-marking program that provided vital information for this thesis research project. As directed by the SWG Chinook salmon OTC evaluation work plan, all hatchery-reared Chinook salmon stocked into the Lake Michigan basin during 2006-2010 were supposed to be mass-marked with a combination of OTC, coded-wire-tags (CWT), and fin-clips to distinguish hatchery and natural origin Chinook salmon.

The SWG Chinook salmon OTC evaluation work plan required that the OTC mark assessment be accomplished by monitoring hatchery QAQC fish and error matrix fish to ensure all hatchery-reared fish were successfully OTC marked. Additionally, error matrix fish were used to quantify the amount of fish being misclassified as either false negatives or false positives. Chinook salmon stocked with double marks (i.e., CWT and/or fin-clips with OTC marks) were used to determine the frequency of false negatives, which is the likelihood of classifying known hatchery origin fish (i.e., OTC marked) as natural origin fish (i.e., OTC unmarked). Chinook salmon stocked with single marks (i.e., CWT and/or fin-clips, but no OTC marks) were used to determine the frequency of false positives, which is the likelihood of classifying a natural origin fish as a hatchery origin fish. Mass-marking projects should use error matrix fish because OTC marks may degrade over time, resulting in detection errors (Claramunt et al. 2006). Failure to incorporate detection errors could lead to significant bias in the true estimate of the proportion of natural origin fish in the population (Szalai and Bence 2002).

There were two general goals of this research project which were closely related to the 2006-2010 OTC study proposed by the SWG. First, we analyzed and summarized the evidence for the accuracy and repeatability of the OTC study. This involved analysis of both the QAQC and age-specific classification error matrix datasets to detect the presence and absence of OTC marks and to determine the validity of our study. We accomplished this by evaluating the permanency and retention of the OTC mark over time, determining the percentage of OTC mark false positive and false negative error rates, and examining the repeatability of OTC mark detection among readers. Second, we examined the data gathered from 2006-2010 to evaluate patterns in the contribution of natural Chinook salmon to the population of Chinook salmon in Lake Michigan. The original plan for the SWG Chinook salmon OTC study was to assess hatchery versus natural origin Chinook contributions at age-1. Our research project expanded the study to compare age-1 contributions to assessments at older ages, which provided information for four age-classes.

The data gathered for this study from 2006-2010 allowed examination of a variety of questions beyond simply assessing the overall contribution of natural origin Chinook salmon to the population at age-1 (the objective of the SWG Chinook salmon OTC study). Specifically, we collected samples from numerous locations throughout Lake Michigan each year, and included samples of older age Chinook salmon in the later years, when older age-classes included marked fish. Therefore, we examined spatial, temporal, and cohort-related patterns in the contribution of natural origin Chinook salmon in Lake Michigan. Thus our research was informed by a more specific set of three research objectives related to our second goal:

1. Do the contributions of natural origin Chinook salmon in Lake Michigan vary among locations within the lake?
2. Do the contributions of natural origin Chinook salmon in Lake Michigan vary among the years of the study?
3. Do the contributions of natural origin Chinook salmon in Lake Michigan vary as a cohort ages in the lake?

Based on previous research (see literature review section), we hypothesized that the proportion of naturally-produced Chinook salmon in Lake Michigan would vary among locations, year-classes (i.e., year-effect), and ages (i.e., age-effect). More specifically for locations, we hypothesized that (1) eastern Lake Michigan would have a higher percentage of naturally-produced Chinook salmon than western Lake Michigan, (2) southern Lake Michigan would have a higher percentage of naturally-produced Chinook salmon than northern Lake Michigan, and (3) southeast Lake Michigan would have the highest percentage of naturally-produced Chinook salmon.

LITERATURE REVIEW

To appreciate the significance of Chinook salmon to the Lake Michigan fishery and ecosystem, it is appropriate to begin with a historical perspective of this large and complex ecosystem. The past century has seen huge changes in this ecosystem, particularly as the Lake Michigan fish community was altered by both unintentional and deliberate introductions of non-native species (Mills et al. 1993a; Ricciardi 2001). Native fish communities in the Great Lakes were relatively stable prior to European settlement, but changed quickly in the mid-1900s (Smith 1968; Hansen and Holey 2002). Until the mid-1900s, the native lake trout (*Salvelinus namaycush)* was the top predator in Lake Michigan (Smith 1968; Hansen and Holey 2002). By the middle of the 20th century, native stocks of lake trout had collapsed due to excessive fishery exploitation and the invasion and predation by sea lamprey (*Petromyzon marinus)* into the Great Lakes (Smith 1968; Lawrie 1970; Hansen and Holey 2002). With the collapse of lake trout, another invasive species, alewife (*Alosa pseudoharengus*), exploded in abundance due to the absence of top predators in the Great Lakes (Smith 1970; O'Gorman and Stewart 1999). By the 1960s, alewife abundance had reached nuisance levels, contributing to 90% of fish biomass in Lake Michigan, and regularly fouling beaches and water intake structures due to periodic, massive die-offs (Brown 1968; Brown 1972; Mills et al. 1993a). Additionally, alewives are believed to have negative effects on native fish populations such as lake trout and yellow perch (*Perca flavescens*) and non-native fish species as well.

The first attempts to introduce Pacific salmon into the Great Lakes basin took place in the late 1800s, however, these early attempts failed to establish a sustainable salmon population and recreational fishery (Tody and Tanner 1966; Collins 1971; Parsons 1973; Emery 1985). In 1967, Chinook salmon also known as "King" salmon, were stocked into Lake Michigan tributaries as part of a Great Lakes basin-wide management effort to re-establish a top predator in Lake Michigan, to enhance the recreational fishery, and to control the nuisance alewife abundance (Tody and Tanner 1966; Brown 1968; Brown 1972; Emery 1985; Mills et al. 1993a). The Michigan Department of Natural Resources (MDNR) stocked Chinook salmon that originated from the lower Columbia River in Oregon and the Green River in Washington (Keller et al. 1990). MDNR managers chose Chinook salmon over other salmonine species because Chinook smolt at a smaller size and younger age, and grow to larger sizes, leading to better cost:benefit ratios than the other candidate species (Hansen and Holey 2002).

This particular attempt at stocking Chinook salmon was extraordinarily successful (Tanner and Tody 2002). Alewife provided an abundant food source, leading to exceptionally rapid growth and high survival of the stocked salmon (Stewart et al. 1981; Emery 1985; Mills et al. 1994). Within a few years, hundreds of thousands of maturing salmon returned to the streams into which they had been stocked as smolts and the world-class recreational fishery that we enjoy today began to develop.

Pacific salmon are a valuable resource, both within their native range in the North Pacific Ocean and in their non-native range in the Laurentian Great Lakes (Claramunt et al. 2012). The stocking of Chinook salmon was not only successful as a biological control for alewife, but converted a degraded fish community into a world-class sport fishery (Keller et al. 1990; Kocik and Jones 1999; Whelan and Johnson 2004; Madenjian et al. 2008; Johnson et al. 2010). Recreational anglers prefer Chinook salmon over other salmonine species because of their large size, fighting ability, and challenge to catch (Benjamin and Bence 2003; Claramunt et al. 2009). Additionally, Chinook salmon are a major part of the Great Lakes multi-billion dollar fishery, which is supported by more than 9.2 million anglers annually (Keller et al. 1990; Hansen and Holey 2002; Tanner and Tody 2002; U.S. Department of the Interior 2006).

From 1967 to 1986, Chinook salmon stocking and harvest rose steadily. Chinook salmon stocking peaked at 7.86 million smolts in 1989, whereas Chinook salmon harvest peaked at 10.4 million pounds in 1986 (Figure 2). During the late 1980s and early 1990s, Chinook salmon in Lake Michigan experienced a bacterial kidney disease (BKD) epizootic, which resulted in a significant decline in Chinook salmon abundance and harvest even though stocking levels remained high until 1998. From 1998 to the present there have been two stocking reductions in Lake Michigan, such that stocking is now less than half of the peak (Figure 2). Chinook salmon stocking was cut from 5.86 million fish in 1998 to 4.2 million fish in 1999 and again stocking was cut from 4.3 million fish in 2005 to 3.2 million fish in 2006. Despite the stocking cuts, Chinook salmon harvest increased from a low of 1.4 million pounds in 1993 to 8.0 million pounds in 2007 and then harvest decreased to 4.3 million pounds in 2011 (Figure 2). Early in the time series, Chinook salmon harvest can be attributed to increases in stocking, however, recent changes are more likely due to a substantial increase in wild Chinook salmon recruitment since the 1980s.

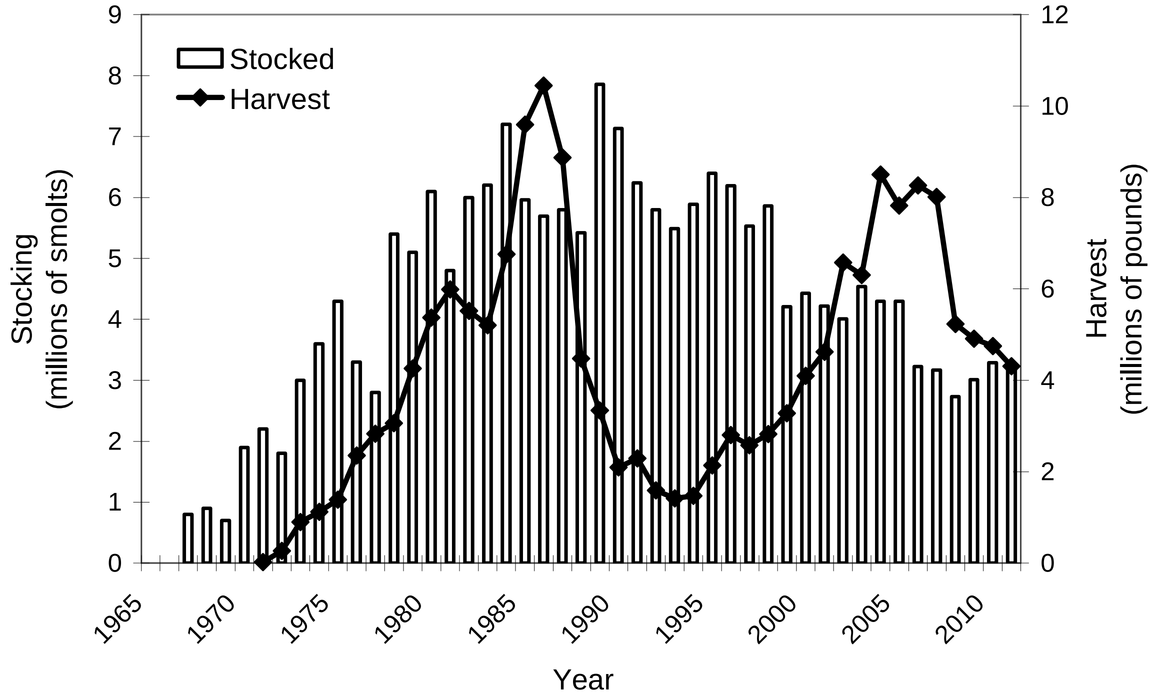

Figure 2.—Lakewide stocking and harvest (recreational and commercial) of Chinook salmon in Lake Michigan, 1967-2011 (Lake Michigan Technical Committee, Salmonid Working Group (SWG), unpublished data).

Claramunt et al. (2012) suggested that “natural reproduction of Pacific salmonines in the Great Lakes has been variable by species, lake, and time, since their initial introductions; however, their ability to reproduce naturally is evident across the Great Lakes.” In Lake Ontario, the proportion of age-3 Chinook salmon estimated to be naturally-produced varied between 1992 and 2005, but averaged 62% (Connerton et al. 2009). In Lake Superior, natural origin Chinook salmon ranged between 50 and 90% during 1989 to 1992 (Peck et al. 1994). In Lake Huron, 15% of the Chinook salmon population was estimated to be naturally-produced before 1995. By 2002, however, the proportion of Lake Huron Chinook salmon estimated to be naturally-produced was roughly 80%, indicating a substantial increase in natural origin Chinook salmon reproduction (Johnson et al. 2010). Similar to Lake Huron, Lake Michigan naturally-produced Chinook salmon smolts have increased steadily since their introduction in 1967 (Claramunt et al. 2012).

Past Lake Michigan Chinook salmon research led us to believe that spatial variations in the contribution of natural origin Chinook salmon might arise because of differences in proximity to good quality spawning habitat. Specifically, we expect higher natural Chinook salmon proportions along the eastern shoreline of Lake Michigan where most natural smolt reproduction is believed to occur. Michigan has a greater number and miles of streams and tributaries that flow into Lake Michigan and provide more high quality spawning habitat for Chinook salmon than the three other states that border Lake Michigan. In general, favorable stream attributes for successful natural reproduction of Pacific salmonines include large coldwater tributaries with consistent flow, well-oxygenated water, and quality substrate comprised of clean gravel or cobble (Raleigh et al. 1984; Raleigh et al. 1986; Groot and Margolis 1991). The majority of Lake Michigan tributaries that meet these characteristics are located on the eastern shoreline (Carl 1982; Carl 1984; Zafft 1992). Carl (1982) found that most Chinook salmon natural reproduction occurred in large trout streams such as the Muskegon, Pere Marquette, and Manistee Rivers, which is similar to findings reported in Pacific Northwest literature wherein Chinook salmon tend to reproduce in larger coldwater streams (Reimers 1968, 1973; Ricker 1972). Carl (1982) also found it interesting that the Pere Marquette River produced the second largest smolt estimate of natural origin Chinook salmon, although the river received no stocked fish and straying was believed to be low. Carl (1982) considered rivers with an average current less than 0.3 m/s could be unsuitable for Chinook salmon natural reproduction because of silt accumulation on the streambed. Carl (1984) found that Lake Michigan Chinook salmon preferred spawning sites with water velocity similar to its parent stock from the Toutle River, Washington.

From 1990-1994, Elliott (1994) studied the early life history of Chinook salmon in eastern Lake Michigan by monitoring and collecting fish samples from nearshore and offshore waters through their first growing season using a variety of gears. During Elliott's study all hatchery-reared Chinook salmon stocked into Lake Michigan waters were marked with a combination of fin-clips, CWT, and OTC. Elliott (1994) found Chinook salmon natural reproduction to be widespread and variable along the eastern shoreline of Lake Michigan. The greatest number of natural origin Chinook salmon appeared to be consistently produced from Michigan rivers in the central region (Holland to Whitehall), which was previously identified by (Carl 1982), followed by the north region (Pentwater to Empire) and south region (New Buffalo to South Haven). Elliott also found natural origin juvenile Chinook salmon accounted for a larger percentage of the sample in the north region as opposed to the south region of Lake Michigan.

According to Avery (1974), Little Scarboro Creek was judged to be the most suitable Wisconsin tributary for coho salmon production that flows into Lake Michigan. However, Cloern (1976) determined that the survival of coho salmon eggs in Little Scarboro Creek to be only 1.4%. Cloern (1976) also determined that the creek did not posses physical characteristics such as water temperature, water velocity, stream discharge, streambed gradient, silt load, stability and permeability of the spawning bed substrate, and dissolved oxygen concentration levels conducive to natural reproduction of salmonids.

On the other hand, Chinook salmon are well known to migrate great distances during their oceanic life stage in the Pacific Ocean (Healey and Groot 1987; Healey 1991). From 1990-2000, 5% of the 8,049 CWT Chinook salmon that were stocked into western Lake Huron were recovered in Lake Michigan. The true extent of migration is currently unknown due to biases in tag recapture and fishing effort (D. Clapp, Michigan DNR Charlevoix Fisheries Research Station, Lake Michigan Research Station Manager, unpublished data). Johnson et al. (2005) reported substantial migration by Chinook salmon between Lakes Michigan and Huron based on absolute numbers of CWT recoveries. The Lake Michigan SWG (2005) reported considerable net migration of hatchery origin Chinook salmon between Lakes Michigan and Huron based on absolute numbers of CWT recoveries as well.

Additionally, Johnson et al. (2007) reported migration by Chinook salmon from Lake Michigan into Lake Huron based on CWT recoveries. Unmarked natural origin Chinook salmon that migrate from Lake Huron into Lake Michigan are probably produced by tributaries in Ontario, Canada, because they have greater access to spawning habitat that are not blocked by dams and are known to sustain natural reproduction, as opposed to Michigan tributaries of Lake Huron that are blocked by dams (Kerr and Perron 1986; Kerr 1987; Kerr et al. 1988).

From 1991 to 2000, Adlerstein et al. (2007) reported that 5.8% of the 10,438 CWT Chinook salmon that were stocked into Lake Huron migrated into Lake Michigan, where they were recovered. However, 462 out of 610 or 75.7% migrated into Lake

Michigan from the MH-1 management unit which directly connects to Lake Michigan waters. Adlerstein et al. (2008) found that Chinook salmon tend to congregate in the southern portion of Lake Michigan during winter and spring, where higher concentrations of prey (e.g., alewife) and warmer water temperatures are located. From May to July, Chinook salmon show a northward progression as nearshore surface waters warm and alewives move to shallow nearshore waters to spawn. During July and August, Chinook salmon move from nearshore to offshore into deeper waters as nearshore waters warm above temperature ranges preferred by both Chinook salmon and alewives. Adlerstein et al. (2008) found Chinook salmon in Lakes Michigan and Huron to exhibit similar northward or coast movement patterns as their Pacific Ocean parent stock.

Additionally, Keller et al. (1990) and Elliott (1993) found that the most influential factors that determine Chinook salmon distribution are temperature and prey. Similar to Adlerstein et al. (2007, 2008), Brandt et al. (1991) found Chinook salmon move away from nearshore areas in the spring and move back into nearshore areas in the fall to coincide with temperature and prey seasonality. Distributions of salmonines in the Great Lakes and Pacific Ocean are both influenced by water temperature (Haynes and Keleher 1986; Haynes et al. 1986; Nettles et al. 1987; Olson et al. 1988; Aultman and Haynes 1993; Höök et al. 2004) and Chinook salmon are most often found at 10-12℃ (Stewart and Ibarra 1991; Walker et al. 2000; Hinke et al. 2005).

Previous evidence presented would also suggest that Chinook salmon wild recruitment would vary substantially from year to year (Figure 1). Chinook salmon recruitment to age-1 depends on a complex array of biotic (e.g., forage base) and abiotic (e.g., spawning habitat, nursery habitat, water quality, water temperature) factors. These complex factors are likely to cause fish populations in Lake Michigan to vary over time (Everhart and Youngs 1981; Schneeberger et al. 1998). Furthermore, Warner et al. (2008) did not find strong evidence for density-dependence in age-1 Chinook salmon growth and condition in Lake Michigan from 1992-1996 and 2001-2005, which would also argue against relatively constant recruitment over time. Similarly, Hansen and Holey (2002) found that mean length and weight of age-1 Chinook salmon collected at the Strawberry Creek weir, WI, between 1983 and 1997 was not density-dependent.

There is conflicting evidence regarding differences in survival of wild Chinook salmon relative to their hatchery counterparts. Elliott (1994) found that natural and hatchery origin Chinook salmon in Lake Michigan seemed to have equal survival from July of their first summer through reaching maturity. Similarly, Hesse (1994) found the proportion of natural origin Chinook salmon at age-3 collected in 1993 to be comparable to the proportion of juveniles in 1990 for the same cohort. In contrast, Johnson et al. (2007) found wild origin Chinook salmon had lower survival than hatchery origin Chinook salmon and a lower spawning-phase return rate. The hatchery origin fish were larger than the wild fish, migrated out of the Au Sable River more quickly, and spent less time in the predator rich beach zone, which Johnson suggested might decrease predation risk (i.e., increase survival). Furthermore, Chinook salmon growth and maturation differences between natural and hatchery origin fish might affect survival rates and relative contributions to the creel (Larsen et al. 2004 and 2006; Shearer et al. 2000 and 2006).

Our literature review suggested there remains considerable uncertainty about the spatial, temporal, and cohort-related patterns in the contribution of wild Chinook salmon. Our study was the first to be able to specifically address these questions for Lake Michigan Chinook, by explicitly examining variation in wild proportions across areas, year-classes, and ages. John Muir once said, “When one tugs at a single thing in nature, he finds it attached to the rest of the world.” This quote is fitting to our research because natural Chinook salmon reproduction is probably affected by several abiotic and biotic factors.

METHODS

Study Area

Chinook salmon samples were targeted throughout Lake Michigan, however, the majority of the lakewide Chinook salmon samples collected came from the 10 most southern management units (Indiana, Illinois, WM-3, WM-4, WM-5, WM-6, MM-5, MM-6, MM-7, and MM-8) because that is where most of the fishing for Chinook salmon occurs (Figure 3). A few additional Chinook salmon samples were collected from WM-2, MM-1, and MM-3 and no samples were collected from WM-1, MM-2, and MM-4.

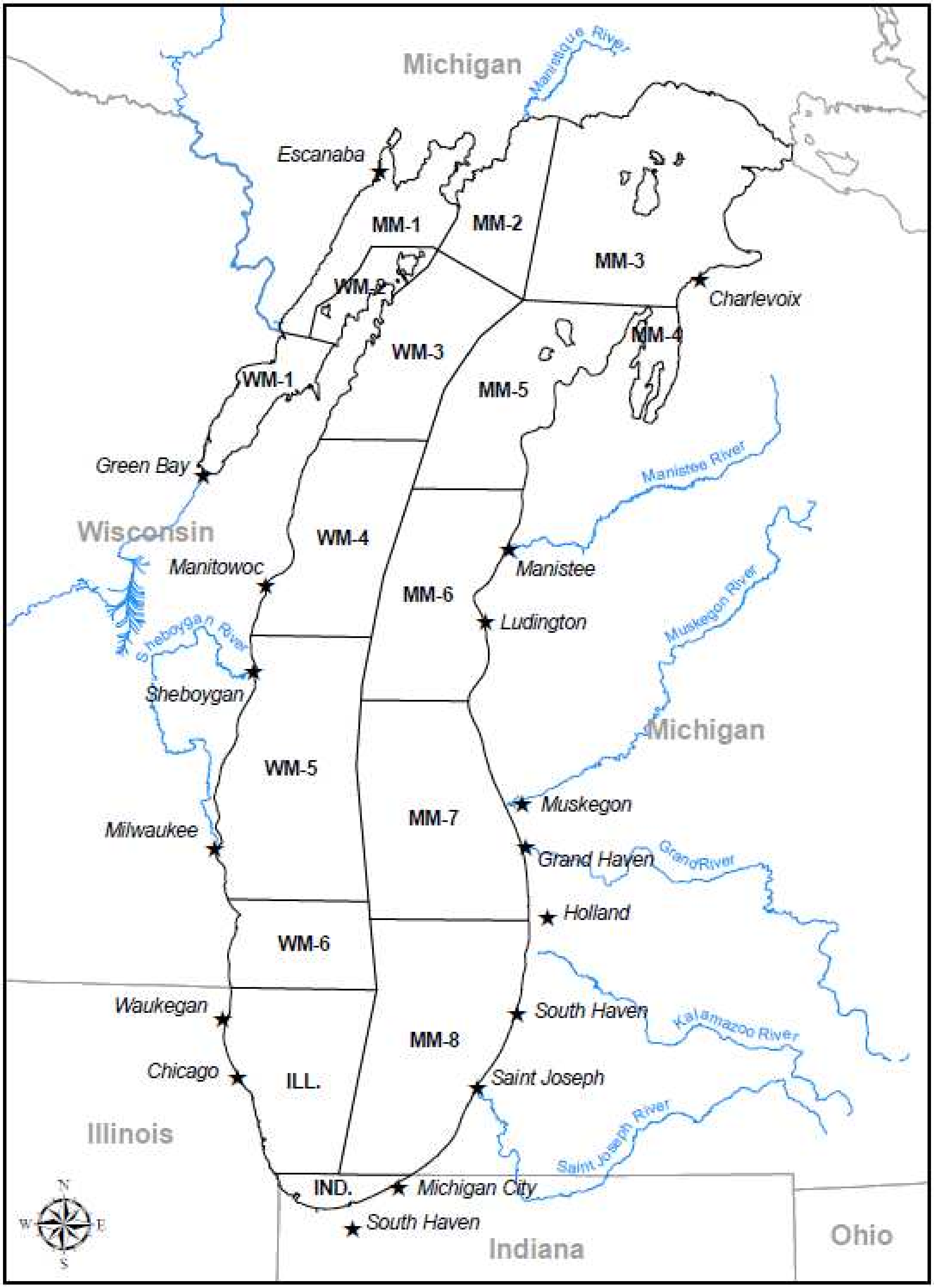

Figure 3.—Lake Michigan management units, large tributaries, and the four bordering states (Illinois, Indiana, Michigan, and Wisconsin). For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

Marking

During 2006-2009, the majority of hatchery-produced Chinook salmon stocked into Lake Michigan were marked exclusively with OTC, coded-wire-tag (CWT) with an adipose fin-clip, or another fin-clip (i.e., single-marked) and with a combination of a CWT with an adipose fin-clip and OTC, or another fin-clip and OTC (i.e., double-marked) to distinguish hatchery and natural origin fish (Table 1). During this period, a total of 12,171,429 Chinook salmon were stocked into Lake Michigan. A total of 1,649,560 were stocked as error matrix fish. Single-marked (457,874) error matrix fish with a CWT and an adipose fin-clip, or another fin-clip, but with no OTC mark were used to determine age-specific false positive error rates. Double-marked (1,191,686) error matrix fish with a combination of a CWT with an adipose fin-clip and OTC mark, or another fin-clip and OTC mark were used to determine age-specific false negative error rates (Table 1). All other fish were single-marked exclusively with OTC, other than an accidental stocking of 157,904 unmarked fish in 2006.

Table 1.—Number of Chinook salmon stocked into Lake Michigan from 2006 to 2010 by Jurisdiction (i.e., Illinois, Indiana, Michigan, and Wisconsin) and by mark type. OTC indicates the fish were marked with the antibiotic oxytetracycline and ADCWT indicates the fish were marked with an adipose fin-clip and a coded-wire-tag. All single- and double-marked error matrix fish are in bold. Illinois accidently stocked 157,904 unmarked fish in 2006. Chinook salmon stocking data was summarized using the Great Lakes Fishery Commission's fish stocking database (http://www.glfc.org/fishstocking/).

Jurisdiction	Year				
Mark type	2006	2007	2008	2009	2010
Illinois					
None	*157,904*	-	-	-	-
OTC	-	168,776	170,269	153,181	175,573
Fin-clip	93,708	-	-	-	-
Fin-clip and OTC	-	83,489	83,740	83,802	75,570
Illinois total	251,612	252,265	254,009	236,983	251,143
Indiana					
OTC	225,131	217,389	215,770	206,714	232,789
Indiana total	225,131	217,389	215,770	206,714	232,789
Michigan					
OTC	1,070,416	1,386,789	1,330,195	1,378,325	939,181
ADCWT	60,851	102,886	99,419	101,010	317,339
ADCWT and OTC	478,574	101,234	100,380	101,200	319,193
Michigan total	1,609,841	1,590,909	1,529,994	1,580,535	1,575,713
Wisconsin					
OTC	1,150,185	1,075,683	685,105	930,037	863,184
Fin-clip and OTC	16,000	37,000	40,500	65,767	-
ADCWT	-	-	-	-	184,527
ADCWT and OTC	-	-	-	-	187,283
Wisconsin total	1,166,185	1,112,683	725,605	995,804	1,234,994
Lake Michigan total	3,252,769	3,173,246	2,725,378	3,020,036	3,294,639

All hatchery-reared Chinook salmon that were marked with OTC feed were fed at a rate of 2% of their body weight per day once the fish reached a minimum size of 250 fish per kg (Younk and Cook 1991; Rutherford et al. 2002; Johnson et al. 2010); feed consisted of 1.5 mm pellets containing 6% Terramycin 100 (Terramycin 100 is composed of 100 g of OTC dehydrate per 454 g of formula). A size threshold was used instead of fish age because fish smaller than 250 fish per kg tend to have more cartilaginous skeletons and will not assimilate the OTC mark regardless of the feeding rate and quantity. Fish were sampled and weighed to determine the food ration prior to OTC feeding. The OTC feeding protocol was administered at 250 mg OTC per kg of body weight per day for two feeding periods of four days, separated by two days of no OTC feeding; following similar methods used in earlier OTC studies (Hesse 1994; Rutherford et al. 2002, Johnson et al. 2010). If additional OTC food was available, then feeding continued with the alternating pattern of four days on, two days off, and four days on until OTC food was no longer available, other constraints prohibited continued feeding, or it became cost-prohibitive to continue OTC feeding (Claramunt et al. 2006).

Once the OTC feeding protocol was completed, but prior to stocking the Chinook salmon according to the stocking plans, hatchery Quality Assurance Quality Control (QAQC) samples were collected from either the hatchery lots or net pens to measure OTC mark assimilation rates. A minimum of 60 randomly selected fish were sampled from each hatchery lot or from each unique rearing group and frozen whole for OTC processing. Because exposure to light can degrade OTC marks (Brothers 1990; Doi and Stoskopf 2000; Johnson et al. 2010), QAQC samples were wrapped in aluminum foil and placed into a zip-lock bag labeled with the appropriate identifying information (Claramunt et al. 2006). Based on stocking levels in 2006 for Illinois (250,000), Indiana (220,000), Michigan (1,600,000), and Wisconsin (1,150,000), the target number of QAQC samples were 60, 60, 360, and 240, respectively, for each jurisdiction. OTC marks can be difficult to detect immediately after the marking period because the marks are usually located on the outside or outer edge of the vertebra and the assimilation of the mark into the calcified structure is not immediate. Accordingly, QAQC samples were supposed to be collected from the hatchery lots as close to the stocking date as possible or when in the net pens. During 2006-2009, all QAQC and error matrix fish samples were processed at the OTC Center, located at the MDNR office in Plainwell, MI.

Field Work

During 2007-2010, Chinook salmon were sampled from the Lake Michigan sport fishery by personnel from Michigan State University, Illinois DNR, Indiana DNR, Michigan DNR, and Wisconsin DNR. Fishery-dependent samples were collected throughout the lake between late April and mid-August, mainly from fishing tournaments. Due to the seasonal movement patterns of Chinook salmon, the majority of samples tended to be collected in the southern part of the lake in the spring, and further north in the summer, with the exception of Illinois collections, which generally occurred in July and August. During this period, Chinook salmon were assumed to be actively feeding in the lake and widely distributed throughout Lake Michigan, and had not begun to stage near their natal streams or stocking sites prior to spawning runs.

The sampling strategy targeted fish across a range of sizes, to ensure representation of multiple age-classes. From 2007 to 2010, Chinook salmon were sampled annually throughout Lake Michigan according to fish length (380-585 mm = age-1 and >586 mm = ages-2 and older; Szalai and Bence 2002). To assist with data collection, Chinook salmon growth rates were assumed to be roughly 25 mm per month. In general, a maximum length of 585 mm was used as a rough guide to ensure enough age-1 fish samples were collected lakewide throughout the summer, however, fish age was later determined by the MDNR using calcified structures (e.g., vertebrae, scales, or otoliths) and confirmed with ADCWT and year-class specific fin-clips for the error matrix fish. Age-1 fish maximum length was extended to roughly 660 mm for the error matrix fish samples collected in rivers in the fall from September to November, in order to account for fish growth. Error matrix fish samples were collected from Lake Michigan during the summer, but the majority were collected in the fall at two Michigan weirs (Little Manistee River Weir and Medusa Weir), two Wisconsin weirs (Strawberry Creek Weir and Root River Weir), and by electrofishing in Illinois harbors. The lakewide total target sample for Lake Michigan in 2007 and 2008 was 1,000 fish because at that time the sampling protocol only called for the collection of age-1 Chinook salmon (Table 2). The lakewide total target sample size in 2009 and 2010 was increased to 3,000 fish because the sampling protocol called for the collection of all ages of Chinook salmon. The 2009 and 2010 collections included ages up to age-3 and age-4 fish, respectively, because OTC mass-marking initiated in 2006 (Table 2).

Table 2.—Target sample sizes for each region based on approximately 1,000 fish per length group.

Region	Management unit	Age-1 target sample size	Age-2 and older target sample size
Northeast	MM5, MM6	200	400
Northwest	WM3, WM4	200	400
Southeast	MM7, MM8	200	400
Southwest	WM5, WM6	200	400
South	IL, IN	200	400
Total		1,000	2,000

All Chinook salmon collected in the field were measured for total length (mm) and weight (g). Additional information measured and recorded in the field and entered into the Chinook salmon OTC database included the bag ID (unique identification number), date, grid, statistical district or management unit, site code, collection method, species, CWT number, fin-clip, lamprey wound classification, and any other applicable information. Sex and maturity status of a subset of collected fish were determined by internal examination of the gonads. Calcified structures (e.g., scales and/or otoliths) were removed from each fish for age-class determination and vertebrae were removed for OTC mark detection. Scales were collected below the dorsal fin and above the lateral line from each fish sampled to determine age-class (Ambrose 1983). We removed roughly 10 vertebrae from the vertebral column posterior of the adipose fin from each Chinook salmon sampled (Figure 4). When possible the vertebral column was collected with skin and flesh attached (Figure 4), but if the sample had been filleted already then it was immediately wrapped in aluminum foil to minimize photolysis of potential OTC marks (Brothers 1990; Doi and Stoskopf 2000; Johnson et al. 2010). Collected specimens were placed in a pre-numbered bag, immediately placed on ice or frozen and transferred back to the laboratory, where they were stored frozen and out of direct light until OTC dissection and processing occurred. Johnson et al. (2010) suggested that even when tail samples are frozen, gradual decay of the OTC mark is possible, therefore, we processed all samples within one year of collection.

Figure 4.—Example of a Chinook salmon OTC tail sample.

Laboratory Work

Vertebrae were examined for OTC presence and absence using a stereo microscope equipped with a stereo epifluorescence illuminator light source with a filter cube (11003V2 BL/VIO C37549; Chroma Technology Corporation), a 5.1-megapixel cooled color digital camera, and Image Pro image capture and analysis software. The Image Pro image capture and analysis software and the camera settings were calibrated to a gamma (0.50) and white light balances (red = 1.380, green = 1.400, and blue = 1.819) to emphasize the OTC mark. We archived a digital image for each unique sample for mark verification and agreement by multiple readers.

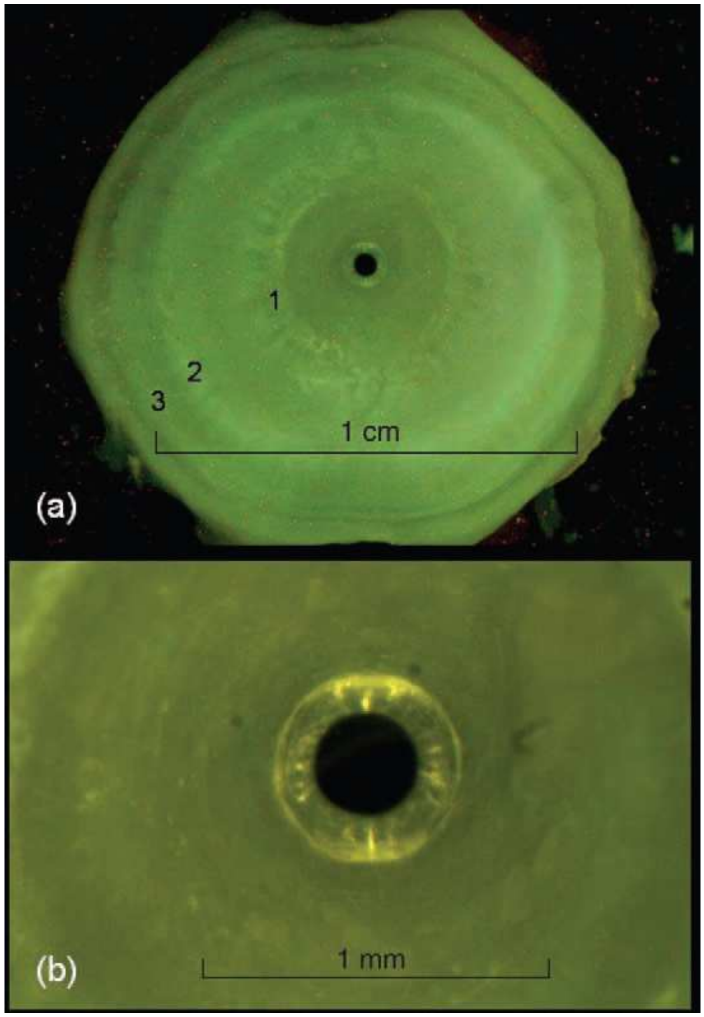

Figure 5.—Vertebra from a 3-year-old Chinook salmon sampled during summer: (a) complete cross section (numbers indicate periods of winter growth) and (b) increased magnification, showing an OTC mark classified as excellent (Johnson et al. 2010).

Similar to the OTC mark processing methods described by Hesse (1994), Elliott (1994), and Johnson et al. (2010), we carefully removed a single vertebra from each partially thawed specimen and cleaned it of all cartilage tissue, leaving only the calcified portion of the vertebra for subsequent examination. Cartilages tissue can cause false OTC mark feedback and block the view of the OTC mark. Following procedures described by Johnson et al. (2010), we took two photographs of each vertebra; one zoomed out image that captured the whole vertebra (Figure 5a) and a second zoomed in image that captured the centrum of the vertebra (Figure 5b), where the OTC mark was expected. The lower magnified image (Figure 5a) for each sample facilitated additional readings of age if necessary and the higher magnified image (Figure 5b) provided a clearer picture of where the OTC mark was expected and aided assessment of OTC mark reader agreement. Winter growth was represented by opaque halos or marks that did not fluoresce, but were more visible if viewed with the ultraviolet light microscope system (Figure 5a).

OTC marks appear as a fluorescent green or yellow colored ring near the centrum of the vertebra in age-1 and older fish (Figure 5b) and towards the outer edge in young-of-the-year fish collected within two months of OTC feeding (e.g., QAQC fish). OTC mark quality is known to vary depending on fish size at marking and amount of OTC food consumed. Therefore, the incidence and quality of OTC marks for each vertebra was subjectively recorded using a five point scale. We ranked the quality of OTC marks as (0) unmarked, (1) poor if the mark around the perimeter of the centrum was less than 25% continuous and the fluorescent band was narrow and dull in color, (2) fair if the mark around the perimeter of the centrum was between 25 and 50% continuous and the fluorescent band was narrow and dull in color, (3) good if the mark around the perimeter of the centrum was between 50 and 75% continuous and the fluorescent band was narrow and bright in color, or (4) excellent if the mark around the perimeter of the centrum was between 75 and 100% continuous and the fluorescent band was wide and bright in color (Figure 6). OTC marks were determined without knowledge of fish characteristics to prevent any bias.

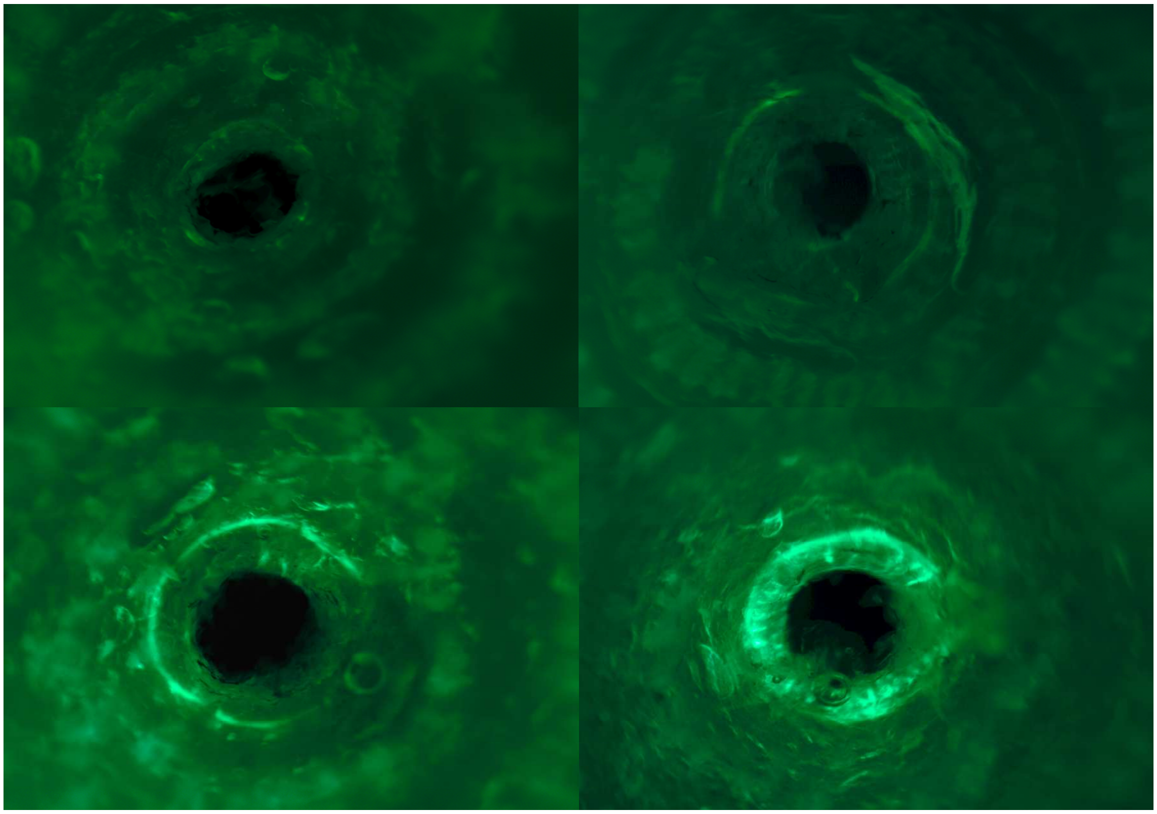

Figure 6.—Example of the subjective OTC mark ranking scale (poor mark—upper left; fair mark—upper right; good mark—lower left; and excellent mark—lower right).

OTC Mark Quality, Assimilation, and Retention

OTC mark quality was analyzed by observing the range in quality of the OTC marks for the 2006-2009 year-classes. Only hatchery origin Chinook salmon with a single or double mark were examined. Average mark quality and the distribution of mark quality among samples were used to assess OTC mark permanency by comparing mark quality in successive years for individual year-classes.

In addition, hatchery QAQC fish were used to measure OTC mark assimilation, and error matrix fish were used to measure OTC mark retention and to estimate lakewide OTC mark false negative and false positive error rates. Chinook salmon stocked with double marks (i.e., CWT and/or fin-clips with OTC marks) were used to determine the frequency of false negatives, which is the likelihood of classifying known hatchery origin fish (i.e., OTC marked) as natural origin fish (i.e., OTC unmarked). Chinook salmon stocked with single marks (i.e., CWT and/or fin-clips, but no OTC marks) were used to determine the frequency of false positives, which is the likelihood of classifying a natural origin fish as a hatchery origin fish.

OTC Mark Repeatability and Reader Agreement

During 2007 and 2008, Chinook salmon vertebrae samples were only processed by one reader at the OTC Center, located at the MDNR office in Plainwell, MI. Therefore OTC mark reader agreement was not examined in 2007 and 2008. During 2009 and 2010, OTC mark reader agreement was examined because Chinook salmon vertebrae samples were processed and OTC marks were determined by two readers. The two readers were both considered experienced OTC mark readers. A sample of 100 vertebrae, 20 from each of the five OTC mark quality categories, were independently examined by two readers for OTC marks and the OTC mark observations were compared to determine repeatability. Comparisons between the two readers were made for (1) agreement on OTC mark quality categories and (2) agreement on the presence and absence of the OTC mark. The results are expressed as percent agreement among the two readers. Additionally, a Kappa test was used to report the level of reader agreement on OTC mark quality categories and on OTC mark presence and absence (Fleiss 1981, cited in Johnson et al. 2010). Agreement measures, such as kappa (K), provide a relative measure of the reliability of the determinations when independent readings by two readers are available. According to Fleiss (1981), Kappa values that exceed 0.75 represent excellent agreement, values of 0.40 to 0.75 represent fair to good agreement, and values below 0.40 represent poor agreement compared with what can be expected by chance alone.

Estimates of Origin by Area, Year-class, and Age

We analyzed the 2006-2010 OTC dataset to evaluate spatial, temporal, and cohort-related patterns in the contribution of natural origin Chinook salmon to the Lake Michigan Chinook salmon fishery and population. The OTC dataset included four cohorts of age-1 fish from the 2006, 2007, 2008, and 2009 year-classes, two cohorts of age-2 fish from the 2007 and 2008 year-classes, two cohorts of age-3 fish from the 2006 and 2007 year-classes, and one cohort of age-4 fish from the 2006 year-class (Appendix A).

All statistical analyses were done using SAS version 9.2. We used generalized linear models that assumed a binomial distribution of OTC mark presence/absence and a logit link function (i.e., logistic regression models). The data were analyzed at different spatial scales including lakewide, by jurisdiction, and by region. The lakewide and jurisdiction level delineations are self-explanatory. The region level analyses was performed both by delineating Lake Michigan into four regions (i.e., northwest, southwest, northeast, and southeast) or into two regions (i.e., north and south). For the four region analysis, the northwest region included management units MM-1, MM-2, WM-1, WM-2, WM-3, and WM-4. The southwest region included management units WM-5, WM-6, and IL. The northeast region included management units MM-3, MM-4, MM-5, and MM-6. The southeast region included management units MM-7, MM-8, and IN. For the two region analysis, the north region included the northwest and northeast regions used for the four region analysis. The south region included the southwest and southeast regions used for the four region analysis.

All factors (e.g., area, year-class, and age) were considered fixed for each analysis (Appendix B). SAS GLIMMIX was used to generate least-square means for the percentage of natural origin Chinook salmon. Pairwise comparisons of least-squares means were conducted using the Tukey-Kramer procedure and results of $P < 0.05$ indicative of significant statistical differences (Kutner et al. 2005). A Tukey-Kramer adjustment is considered a conservative approach to protect the overall error rate when multiple comparison tests are performed. If statistically significant interactions were determined, then the SAS slicediff function was used to analyze the simple effects (e.g., comparisons among regions for each age of fish), instead of the main effects.

Analyses were based on the uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery for the 2006-2009 year-classes because error rates can not be assigned to individual observations or fish. This can be justified because error rates were less than one percent overall during our study. We also did not correct for the fact that 157,904 out of 3,252,769 (4.85%) of the Chinook salmon from the 2006 year-class were stocked into Lake Michigan waters by Illinois DNR without a known hatchery mark, again, because the marking error rate can not be assigned to individual observations or fish. We excluded age-2 Chinook salmon from the 2006 year-class from the statistical analysis due to the maximum length limit of 624 mm that was used for the fish collection protocol in 2007 and 2008 that was only designed to target age-1 fish, not age-2 and older fish. Additionally, we determined that there was a size-at-age difference between natural and hatchery origin Chinook salmon at age-1 and age-2 and that natural fish are shorter than hatchery fish. Therefore, we believed the percentage of age-2 natural Chinook salmon from the 2006 year-class was biased high and was not considered for our statistical analyses.

Estimates of Size-at-age and Maturity-at-age

Differences in size-at-age and proportions mature-at-age between hatchery and natural origin fish were also assessed. The statistical analyses performed were the same as those described above in the estimates of origin section. For the size-at-age data, a normal distribution and an identity link function were assumed for the model. For the maturation data, a binomial distribution and logit link function were assumed for the model. These analyses had smaller sample sizes when fish sex and/or maturity were considered as factors because fish sex and maturity information was not recorded on all fish.

RESULTS

OTC Mark Quality, Assimilation, and Retention

For the 2,026 single-marked Chinook salmon – those determined to have an OTC mark – poor quality OTC marks constituted 14.6% of the 2006 year-class, 7.7% of the 2007 year-class, 2.1% of the 2008 year-class, and 5.3% of the 2009 year-class (Table 3). Additionally, when all 2,026 single-marked fish were pooled, 7.7% of the marks were classified as poor, 24.2% were classified as fair, 38.0% were classified as good, and 30.1% were classified as excellent. There was a tendency for OTC mark quality to be higher in the later year-classes.

Table 3.—Distributions of OTC mark quality classifications (percent) for single-marked fish by year-class and age. Sample sizes are shown in parentheses.

	Year-class			
	2006	2007	2008	2009
Age	Mark Quality	Mark Quality	Mark Quality	Mark Quality
1	Poor = 15.5 Fair = 33.6 Good = 38.0 Excellent = 12.9 (n = 271)	Poor = 6.4 Fair = 26.5 Good = 37.1 Excellent = 29.9 (n = 264)	Poor = 0.8 Fair = 8.8 Good = 34.0 Excellent = 56.3 (n = 238)	Poor = 5.3 Fair = 16.5 Good = 39.8 Excellent = 38.4 (n = 284)
2	--	Poor = 10.0 Fair = 31.4 Good = 40.0 Excellent = 18.6 (n = 210)	Poor = 3.1 Fair = 15.0 Good = 40.8 Excellent = 41.2 (n = 294)	
3	Poor = 13.5 Fair = 33.9 Good = 33.9 Excellent = 18.7 (n = 230)	Poor = 6.9 Fair = 29.6 Good = 42.1 Excellent = 21.3 (n = 216)		
4	Poor = 15.8 Fair = 47.4 Good = 21.1 Excellent = 15.8 (n = 19)			

For the 889 double-marked Chinook salmon – those known to have an OTC mark – poor quality OTC marks constituted 13.7% of the 2006 year-class, 8.6% of the 2007 year-class, 0.5% of the 2008 year-class, and 0.6% of the 2009 year-class (Table 4). When all 889 double-marked fish were pooled, 7.0% of the marks were classified as poor, 22.9% were classified as fair, 34.0% were classified as good, and 36.1% were classified as excellent. There was a tendency for OTC mark quality to be higher in the later year-classes.

Table 4.—Distributions of OTC mark quality classifications (percent) for double-marked error matrix fish by year-class and age. Sample sizes are shown in parentheses.

	Year-class			
	2006	**2007**	**2008**	**2009**
Age	Mark Quality	Mark Quality	Mark Quality	Mark Quality
1	Poor = 15.7 Fair = 43.9 Good = 34.8 Excellent = 5.6 (n = 198)	Poor = 2.2 Fair = 33.3 Good = 35.6 Excellent = 28.9 (n = 45)	Poor = 0.0 Fair = 5.2 Good = 29.6 Excellent = 65.2 (n = 115)	Poor = 0.6 Fair = 8.6 Good = 30.9 Excellent = 59.9 (n = 162)
2	--	Poor = 12.4 Fair = 30.1 Good = 41.6 Excellent = 15.9 (n = 113)	Poor = 1.3 Fair = 8.7 Good = 25.0 Excellent = 65.0 (n = 80)	
3	Poor = 8.3 Fair = 30.6 Good = 44.4 Excellent = 16.7 (n = 72)	Poor = 7.2 Fair = 18.6 Good = 30.9 Excellent = 43.3 (n = 97)		
4	Poor = 14.3 Fair = 14.3 Good = 57.1 Excellent = 14.3 (n = 7)			

A total of 908 false negative and 302 false positive error matrix fish were sampled and analyzed for OTC marks by MDNR and MSU personnel. The false negative error rates varied between 0.00 and 12.50% and the false positive error rates were either 0.00 or 2.78% for the ten age and year-class combinations (Table 5). False negative and false positive error rates only occurred during the 2006 and 2007 year-classes. The age-4 fish for the 2006 year-class had the highest error rate, albeit due to a small sample size of false negative error matrix fish for that specific age and year-class combination. Additionally, there were only 82 age-4 fish for the 2006 year-class sampled and age-4 fish only represent a small proportion of the Lake Michigan Chinook salmon fishery or population (Appendix A). During our study the overall false negative (0.77%) and false positive (0.66%) error rates were both less than one percent.

Table 5.—Percentage of false negative and false positive error matrix fish by year-class and age. Sample sizes are shown in parentheses.

	Year-class			
	2006	**2007**	**2008**	**2009**
Age	False - / False +	False - / False +	False - / False +	False - / False +
1	1.49 / 0.00 (201 / 26)	0.00 / 2.78 (45 / 72)	0.00 / 0.00 (115 / 60)	0.00 / 0.00 (162 / 98)
2	0.00 / 0.00 (12 / 1)	0.88 / 0.00 (114 / 1)	0.00 / 0.00 (80 / 0)	
3	1.37 / 0.00 (73 / 40)	1.02 / 0.00 (98 / 2)		
4	12.50 / 0.00 (8 / 2)			

During our study, a total of 1,785 Quality Assurance Quality Control (QAQC) Chinook salmon samples were collected from hatcheries located in Michigan, Wisconsin, Illinois, and Indiana and analyzed for OTC marks by the MDNR. The percentage of OTC marked QAQC Chinook salmon varied between 81.5 and 100.0% for the four year-classes (Table 6). Overall, 92.5% of the QAQC fish for the 2006 to 2009 year-classes were determined to have OTC marks. The Chinook salmon from the 2007 year-class had a lower percentage of OTC marked QAQC fish, however, we are not concerned that they affected our results.

Table 6.—Percentage of OTC marked quality assurance quality control (QAQC) Chinook salmon by year-class. Sample sizes are shown in parentheses.

Year-class			
2006	**2007**	**2008**	**2009**
100.0 (n = 357)	81.5 (n = 562)	95.5 (n = 359)	97.2 (n = 507)

OTC Mark Repeatability and Reader Agreement

Comparisons between the two readers were made for (1) agreement on OTC mark quality categories and (2) agreement on the presence and absence of the OTC mark. For 2009, 70 out of 100 (70%) vertebrae samples were assigned to the same OTC mark quality category by the two readers; reader agreement was considered fair to good as indicated by a Kappa value of 0.63. For 2010, 67 out of 100 (67%) vertebrae samples were assigned to the same OTC mark quality category by the two readers; again, reader agreement was considered fair to good as indicated by a Kappa value of 0.59.

Agreement for the OTC mark presence and absence was obtained for 95% of the vertebrae samples for both 2009 and 2010. Overall, reader agreement for OTC mark presence and absence was considered excellent as indicated by a Kappa value of 0.86 for both years.

Estimates of Origin by Area, Year-class, and Age

During our study, a total 5,192 Chinook salmon tails were sampled lakewide from Lake Michigan and used to determine estimates of fish origin (i.e., natural or hatchery) by area, year-class, and age (Appendix A). For the 2006 year-class, a total of 1,400

Chinook salmon tail samples were collected for three age-classes. For the 2007 year-class, a total of 1,706 Chinook salmon tail samples were collected for three age-classes. For the 2008 year-class, a total of 1,462 Chinook salmon tail samples were collected for two age-classes. For the 2009 year-class, a total of 624 age-1 Chinook salmon tail samples were collected.

The uncorrected proportion of natural origin Chinook salmon lakewide ranged from 53.52 to 56.92% for age-1, 62.90 to 69.05% for age-2, 62.11 to 66.62% for age-3, and were 76.83% for age-4 (Table 7). The corrected natural origin Chinook salmon proportions were very similar and ranged from 53.52 to 56.07% for age-1, 62.35 to 69.05% for age-2, 61.47 to 65.71% for age-3, and was 67.23% for age-4 (Table 8).

The age-specific classification error matrix used for our study resulted in six corrections for the 2006 and 2007 year-classes and zero corrections for the 2008 and 2009 year-classes (Table 8). There were five corrections for false negative fish and one correction for false positive fish. Five out of the six corrections were less than 1.30%. The age-4 fish from the 2006 year-class had a false negative correction of 9.60%.

Table 7.—Uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by year-class and age. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	56.92 (53.05-60.79)	54.01 (49.93-58.08)	53.52 (49.20-57.84)	54.49 (50.58-58.39)
2	--	62.90 (58.92-66.88)	69.05 (66.11-71.99)	
3	66.62 (63.10-70.14)	62.11 (58.12-66.09)		
4	76.83 (67.70-85.96)			

Table 8.—Corrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by year-class and age. An age-specific classification error matrix was used to correct for age-specific false positive and false negative error rates. The proportions underlined signify that they were adjusted by the age-specific classification error matrix. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	<u>56.07</u> (52.19-59.94)	<u>55.28</u> (51.22-59.35)	53.52 (49.20-57.84)	54.49 (50.58-58.39)
2	--	<u>62.35</u> (58.35-66.34)	69.05 (66.11-71.99)	
3	<u>65.71</u> (62.16-69.25)	<u>61.47</u> (57.48-65.47)		
4	<u>67.23</u> (57.07-77.39)			

At the lakewide level, the two-way interaction between year-class and age was non-significant ($F(2, 5{,}187) = 1.59$, $p = 0.21$) and the main effect of year-class was marginally non-significant ($F(3, 5{,}189) = 2.43$, $p = 0.06$). However, the main effect of age was significant ($F(3, 5{,}189) = 20.93$, $p < 0.01$). The proportion of wild age-1 Chinook salmon (54.79%) was significantly less than the proportions of wild age-2 fish (67.20%; $t(5{,}189) = 6.55$, $p < 0.01$), wild age-3 fish (64.63%; $t(5{,}189) = 5.12$, $p < 0.01$), and wild age-4 fish (75.24%; $t(5{,}189) = 3.39$, $p < 0.01$). The proportions of wild age-2 and age-3 fish ($t(5{,}189) = 1.17$, $p = 0.64$), wild age-2 and age-4 fish ($t(5{,}189) = 1.41$, $p = 0.49$), and wild age-3 and age-4 fish ($t(5{,}189) = 1.88$, $p = 0.24$) were all similar (Figure 7).

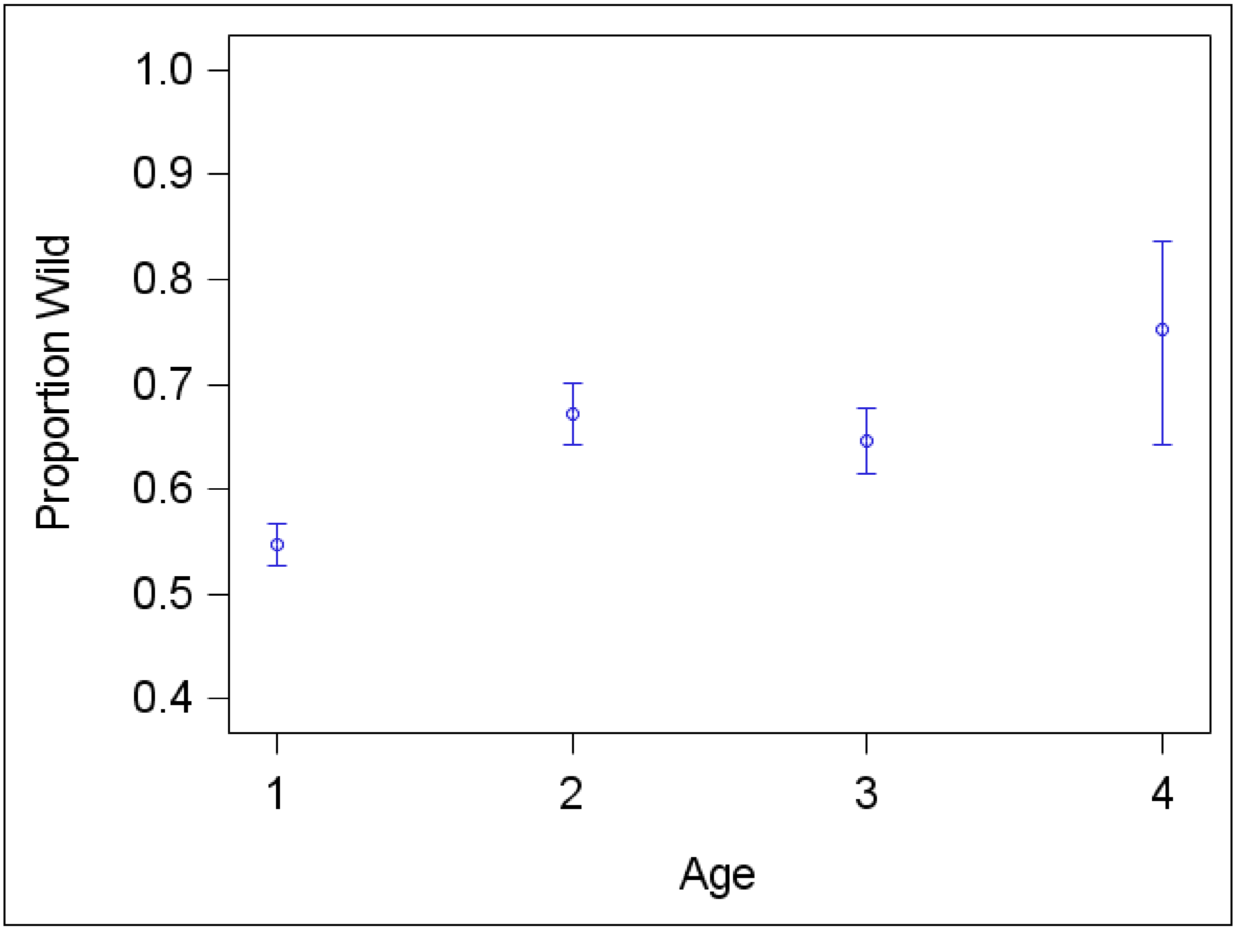

Figure 7.—Proportion of wild Chinook salmon in Lake Michigan by age.

At the jurisdiction level, the three-way interaction between jurisdiction, year-class, and age was non-significant ($F(5, 5{,}158) = 1.83$, $p = 0.10$). The two-way interaction between jurisdiction and age was the only significant interaction ($F(8, 5{,}165) = 2.27$, $p = 0.02$). The proportion of wild age-1 Chinook salmon was significantly greater in Illinois waters (70.92%) than in Wisconsin waters (48.40%; $t(5{,}165) = 3.56$, $p < 0.01$). The proportion of wild age-1 Chinook salmon was also significantly greater in Michigan waters (59.87%) than in Wisconsin waters (48.40%; $t(5{,}165) = 5.36$, p < 0.01). Illinois and Indiana fish do not have any apparent age-effects, likely due to small sample sizes. For Michigan waters, the proportion of wild age-1 Chinook salmon (59.87%) was only significantly less than the proportion of wild age-3 Chinook salmon (67.80%; $t(5,165) = 2.75$, $p = 0.03$). For Wisconsin waters, the proportion of wild age-1 Chinook salmon (48.40%) was significantly less than the proportions of wild age-2 fish (69.80%; $t(5,165) = 7.82$, $p < 0.01$), wild age-3 fish (63.73%; $t(5,165) = 5.17$, $p < 0.01$), and wild age-4 fish (74.43%; $t(5,165) = 3.04$, $p = 0.01$; Figure 8).

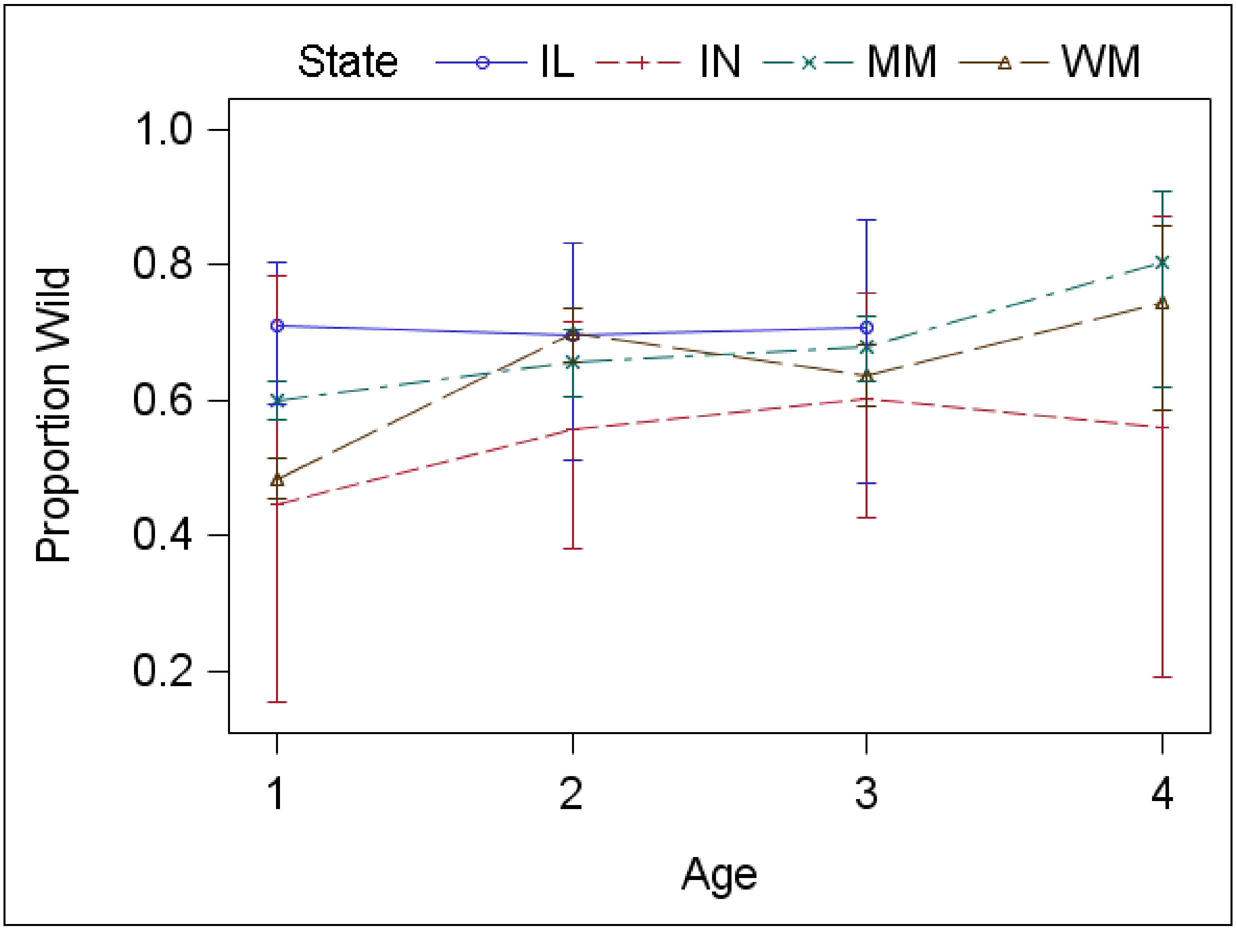

Figure 8.—Proportion of wild Chinook salmon in Lake Michigan for the Illinois (IL), Indiana (IN), Michigan (MM), and Wisconsin (WM) jurisdictions by age.

We also compared Michigan and Wisconsin waters only to avoid the small sample sizes of fish for Illinois and Indiana and to compare the contribution of natural origin Chinook salmon between eastern and western Lake Michigan. Again, we determined that the three-way interaction between jurisdiction, year-class, and age was non-significant ($F(2, 4{,}514) = 0.09$, $p = 0.91$). The two-way interaction between jurisdiction and age was once again significant ($F(3, 4{,}518) = 4.96$, $p < 0.01$). The Michigan and Wisconsin age-effect results were the same as those obtained when all jurisdictions were included. The proportion of wild age-1 Chinook salmon was significantly greater in Michigan waters (59.87%) than in Wisconsin waters (48.40%; $t(4{,}518) = 5.36$, $p < 0.01$). The proportion of wild age-2 Chinook salmon in Michigan (65.54%) and Wisconsin (69.80%) waters were similar ($t(4{,}518) = 1.32$, $p = 0.19$). The proportion of wild age-3 Chinook salmon in Michigan (67.80%) and Wisconsin (63.73%) waters were similar ($t(4{,}518) = 1.18$, $p = 0.24$). The proportion of wild age-4 Chinook salmon in Michigan (80.25%) and Wisconsin (74.43%) waters were similar ($t(4{,}518) = 0.56$, $p = 0.57$; Figure 9).

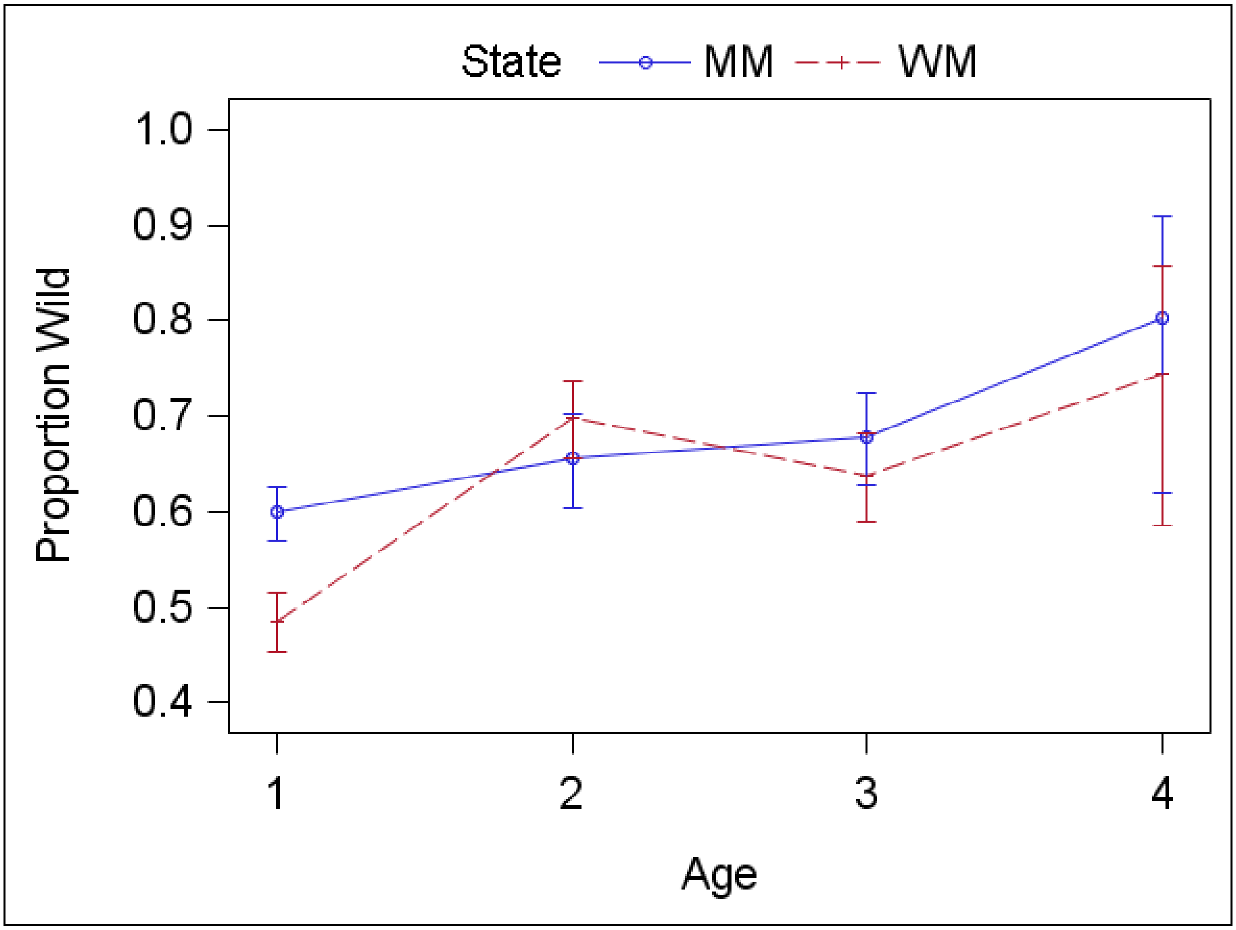

Figure 9.—Proportion of wild Chinook salmon in Lake Michigan for the Michigan (MM) and Wisconsin (WM) jurisdictions by age.

At the region level for the two-region analysis, the three-way interaction between region, year-class, and age was non-significant (F(2, 5,176) = 0.36, p = 0.70). The contributions of wild Chinook salmon to northern and southern Lake Michigan were similar for all four ages of fish (F(3, 5,178) = 0.35, p = 0.79); Figure 10). However, the north and south regions showed an age-effect (F(3, 5,178) = 19.04, p < 0.01), which is consistent with the lakewide and jurisdiction analyses. In the north region, the proportion of wild age-1 Chinook salmon (52.95%) was significantly less than the proportions of wild age-2 fish (67.53%; t(5,178) = 4.02, p < 0.01) and wild age-3 fish (64.10%; t(5,178) = 3.24, p = 0.01). In the south region, the proportion of wild age-1

Chinook salmon (55.23%) was significantly less than the proportions of wild age-2 fish (67.10%; $t(5{,}178) = 5.32$, $p < 0.01$) and wild age-3 fish (64.77%; $t(5{,}178) = 4.03$, $p < 0.01$). All other within region and age comparisons were similar (Figure 10).

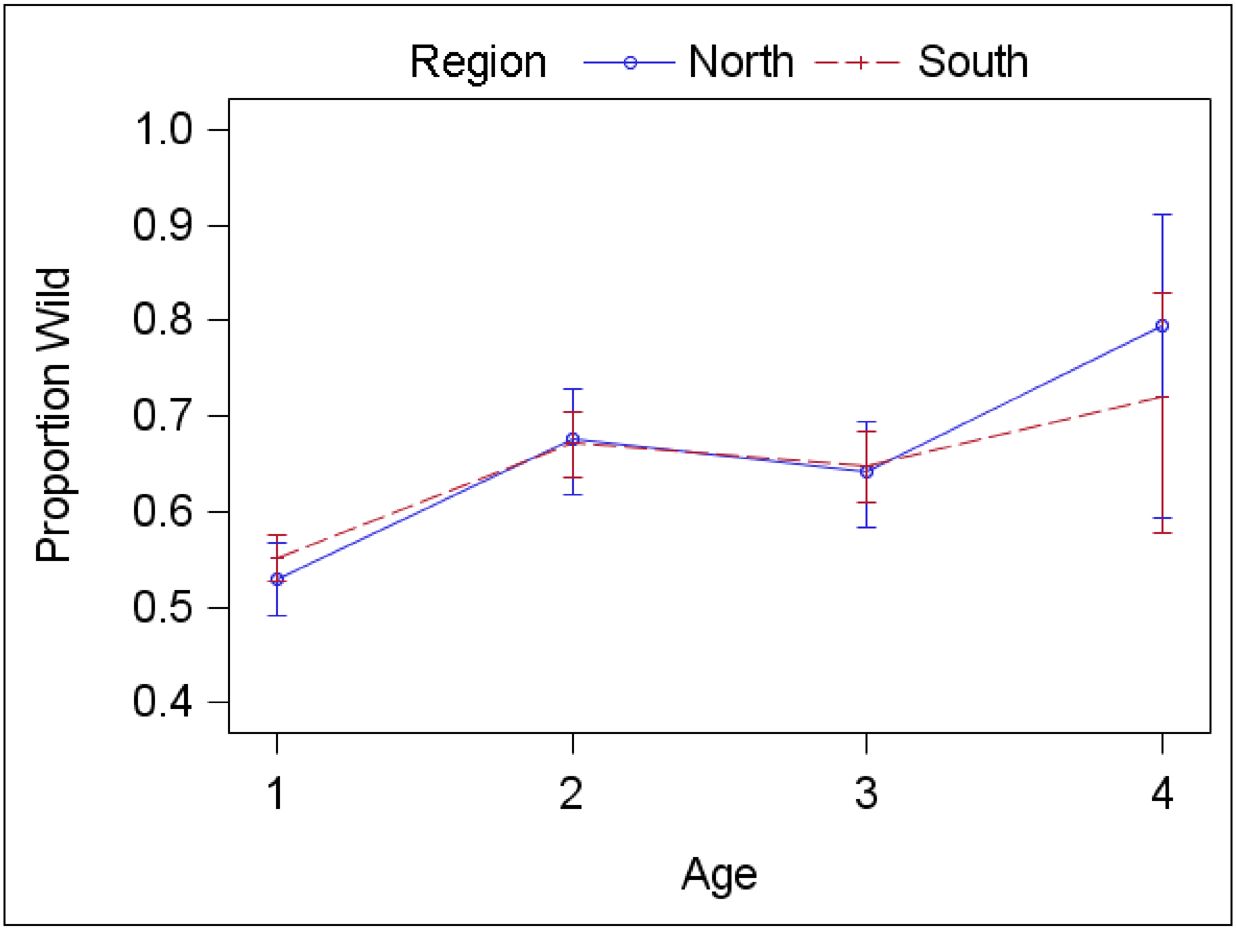

Figure 10.—Proportion of wild Chinook salmon in Lake Michigan for the north and south regions by age.

At the region level for the four-region analysis, the three-way interaction between region, year-class, and age was non-significant ($F(6, 5{,}156) = 1.91$, $p = 0.08$). The two-way interaction between region and age was significant ($F(9, 5{,}164) = 3.40$, $p < 0.01$). The northeast, northwest, and southwest regions all had an age-effect, which is consistent with the lakewide, jurisdiction, and two-region analyses; however, the southeast region did not have an age-effect (Figure 11). In the northeast region, the proportion of wild age-1 Chinook salmon (53.87%) was significantly less than the proportions of wild age-2 fish (70.23%; $t(5,176) = 3.10$, $p = 0.01$) and wild age-3 fish (70.76%; $t(5,176) = 3.51$, $p < 0.01$). In the northwest region, the proportion of wild age-1 Chinook salmon (53.41%) was significantly less than the proportions of wild age-2 fish (67.34%; $t(5,176) = 3.73$, $p < 0.01$) and wild age-3 fish (64.05%; $t(5,176) = 2.66$, $p = 0.04$). In the southwest region, the proportion of wild age-1 Chinook salmon (49.25%) was significantly less than the proportions of wild age-2 fish (71.40%; $t(5,176) = 7.65$, $p < 0.01$), wild age-3 fish (65.51%; $t(5,176) = 4.97$, $p < 0.01$), and wild age-4 fish (74.29%; $t(5,176) = 2.77$, $p = 0.03$; Figure 11). All other within region and age comparisons were similar (Figure 11).

The proportion of wild age-1 Chinook salmon was significantly greater in the southeast region (60.33%) than in the southwest region (49.25%; $t(5,176) = 4.48$, $p < 0.01$). Conversely, the proportion of wild age-2 Chinook salmon was significantly less in the southeast region (61.73%) than in the southwest region (71.40%; $t(5,176) = 3.35$, $p < 0.01$). All other region and age comparisons were similar (Figure 11).

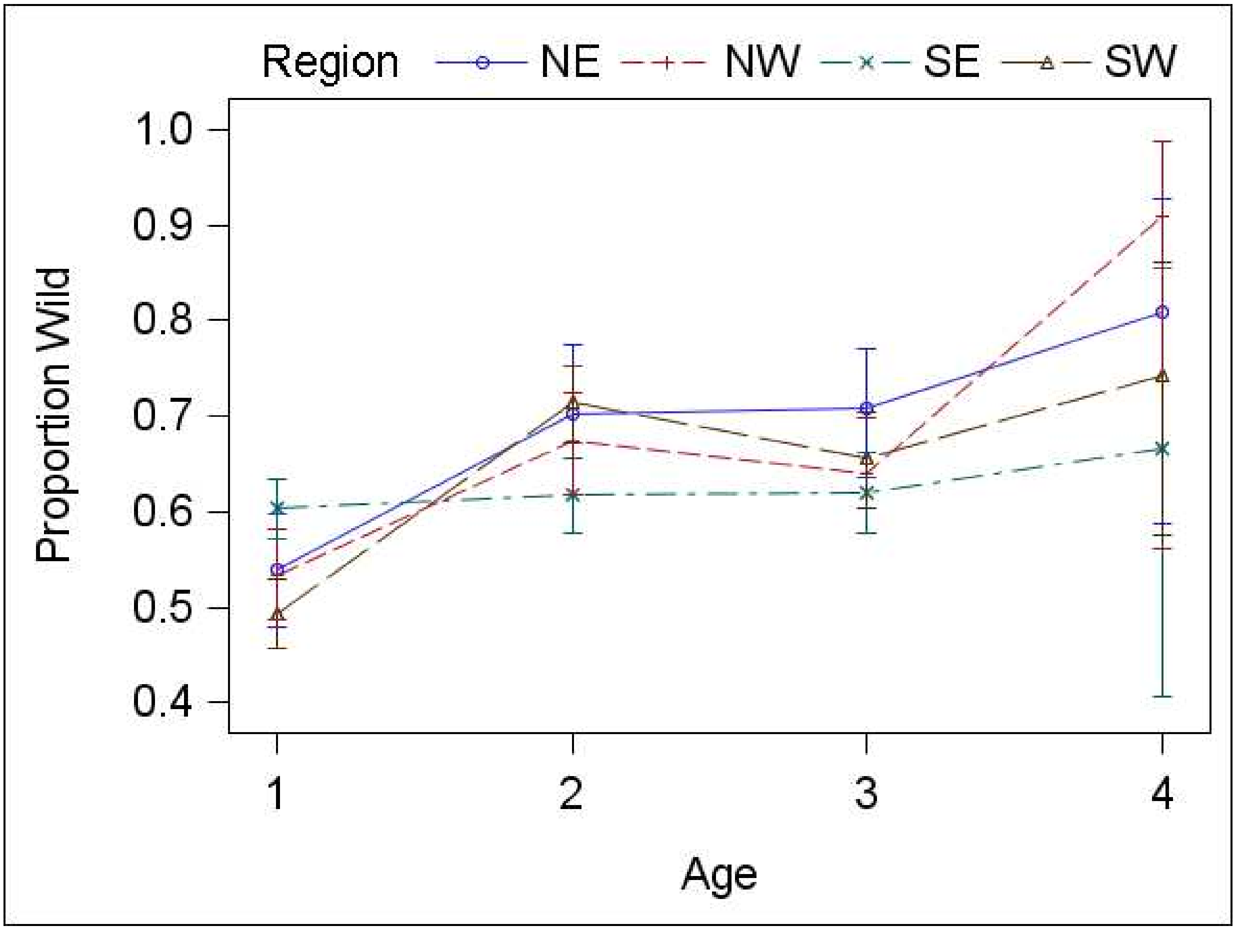

Figure 11.—Proportion of wild Chinook salmon in Lake Michigan for the northeast (NE), northwest (NW), southeast (SE), and southwest (SW) regions by age.

Estimates of Size-at-age

A total of 5,168 hatchery and natural origin Chinook salmon were sampled and analyzed for differences in length (mm) for nine age and year-class combinations. The length-at-age differences between hatchery and natural origin Chinook salmon were greatest for age-1 and age-2 fish and no longer apparent for age-3 and age-4 fish (Tables 9 and 10; Figure 12).

Table 9.—Hatchery origin Chinook salmon average length-at-age (mm) by year-class collected from the Lake Michigan sport fishery. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	420.8 (413.3 - 428.3)	422.6 (415.0 - 430.0)	439.0 (431.0 - 446.9)	430.8 (423.5 - 438.0)
2	--	668.0 (659.5 - 676.4)	668.5 (661.3 - 675.6)	
3	794.9 (786.9 - 803.0)	812.9 (804.6 - 821.2)		
4	867.6 (838.8 - 896.4)			

Table 10.—Natural origin Chinook salmon average length-at-age (mm) by year-class collected from the Lake Michigan sport fishery. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	399.0 (392.4 - 405.5)	390.5 (383.6 - 397.5)	403.9 (396.5 - 411.3)	387.9 (381.3 - 394.5)
2	--	664.3 (657.8 - 670.8)	637.6 (632.9 - 642.4)	
3	794.8 (789.1 - 800.5)	808.7 (802.2 - 815.3)		
4	863.2 (847.7 - 878.7)			

The three-way interaction between fish origin, year-class, and age for length was marginally non-significant ($F(2, 5,150) = 2.74$, $p = 0.06$). We determined that hatchery origin age-1 fish were larger than the natural origin age-1 fish for the 2006 year-class ($t(5,150) = 4.30$, $p < 0.01$), the 2007 year-class ($t(5,150) = 6.14$, $p < 0.01$), the 2008 year-class ($t(5,150) = 6.33$, $p < 0.01$), and the 2009 year-class ($t(5,150) = 8.55$, $p < 0.01$). Additionally, hatchery origin age-2 fish were larger than the natural origin age-2 fish for the 2008 year-class ($t(5,150) = 7.03$, $p < 0.01$; Tables 9 and 10; Figure 12). All other fish origin, year-class, and age comparisons for average length were similar (Figure 12).

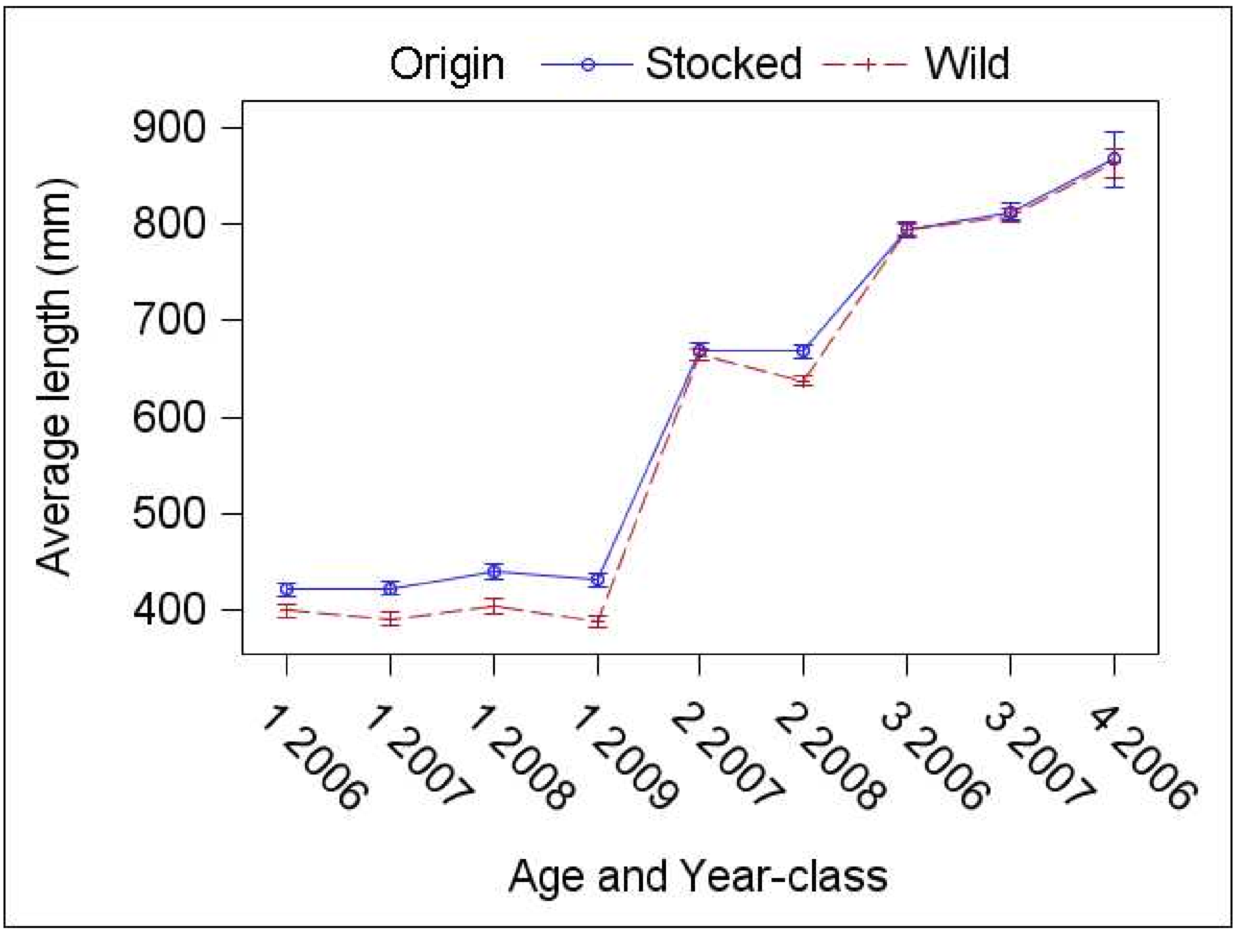

Figure 12.—Lake Michigan stocked and wild origin Chinook salmon average length (mm) by age and year-class.

The two-way interaction between fish origin and age was significant ($F(3, 5{,}154) = 7.03$, $p < 0.01$), when year-classes were aggregated together by age. Age-1 hatchery origin Chinook salmon (428.18 mm) were larger than the age-1 natural origin Chinook salmon (395.06 mm; $t(5{,}154) = 12.66$, $p < 0.01$). Age-2 hatchery origin Chinook salmon (663.76 mm) were larger than the age-2 natural origin Chinook salmon (645.71 mm; $t(5{,}154) = 4.32$, $p < 0.01$). Age-3 hatchery origin Chinook salmon (808.79 mm) were larger than the age-3 natural origin Chinook salmon (796.30 mm; $t(5{,}154) = 2.90$, $p < 0.01$). However, age-4 hatchery origin Chinook salmon (877.96 mm) were not significantly larger than the age-4 natural origin Chinook salmon (862.33 mm; $t(5{,}154) = 0.91$, $p = 0.36$; Figure 13).

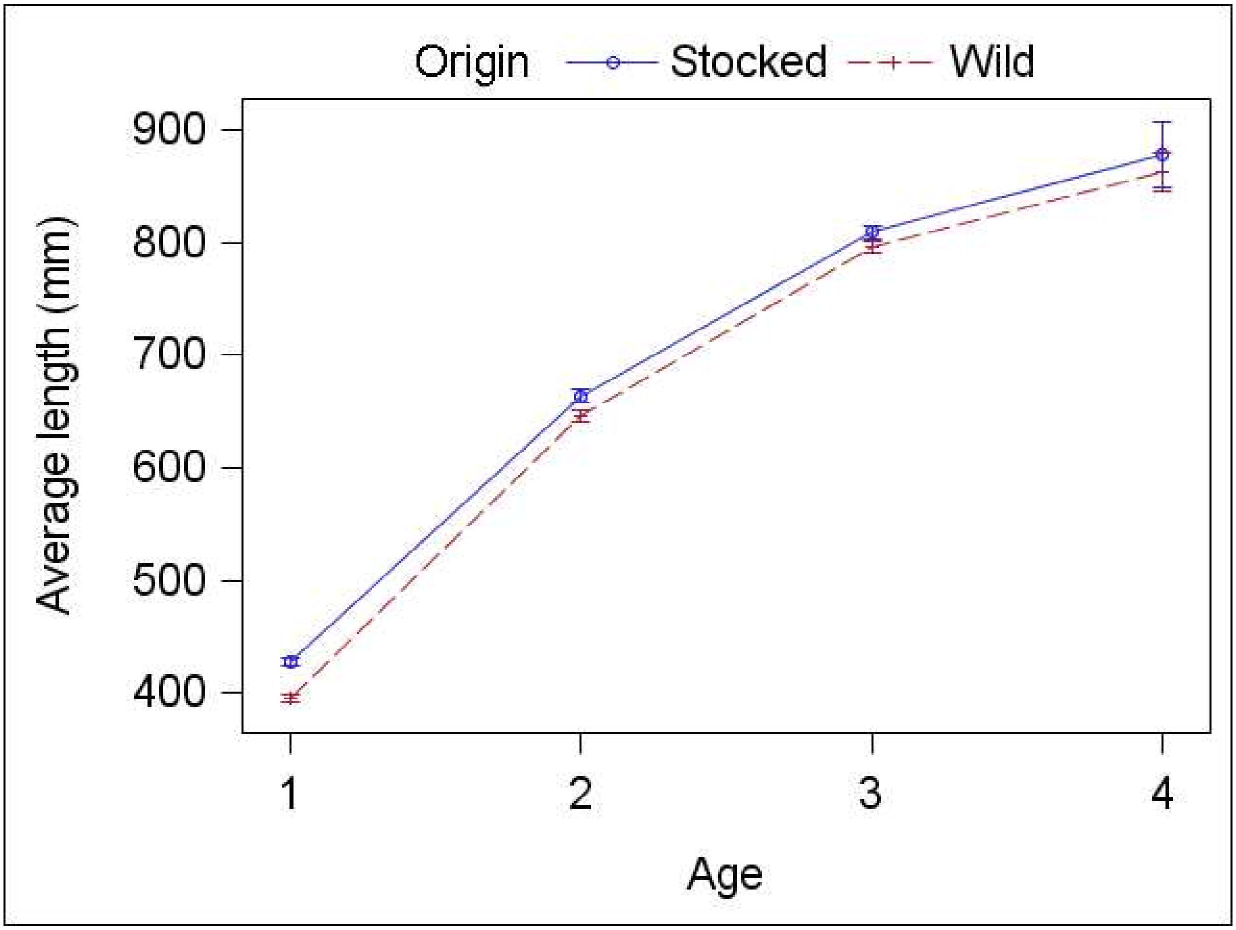

Figure 13.—Lake Michigan stocked and wild origin Chinook salmon average length (mm) by age.

A total of 4,887 hatchery and natural origin Chinook salmon were sampled and analyzed for differences in weight (g) for nine age and year-class combinations. The weight-at-age differences between hatchery and natural origin Chinook salmon were greatest for age-1, age-2, and age-3 fish and no longer apparent for age-4 fish, possibly due to a small sample size (Tables 11 and 12; Figure 14).

Table 11.—Hatchery origin Chinook salmon average weight-at-age (g) by year-class collected from the Lake Michigan sport fishery. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	705.6 (597.1-814.2)	717.2 (609.5-824.9)	886.2 (772.4-999.9)	776.2 (672.1-880.2)
2	--	3,098.6 (2,978.8-3,218.3)	2,958.6 (2,855.7-3,061.5)	
3	5,491.0 (5,376.5-5,605.5)	5,374.1 (5,254.9-5,493.2)		
4	6,405.8 (6,003.6-6,808.0)			

Table 12.—Natural origin Chinook salmon average weight-at-age (g) by year-class collected from the Lake Michigan sport fishery. 95% confidence intervals are shown in parentheses.

	Year-class			
Age	**2006**	**2007**	**2008**	**2009**
1	593.9 (498.1-689.7)	551.8 (453.4-650.1)	709.2 (597.9-820.5)	607.6 (513.1-702.1)
2	--	2,988.8 (2,896.7-3,080.9)	2,410.6 (2,342.1-2,479.1)	
3	5,343.5 (5,263.2-5,423.7)	5,135.8 (5,040.3-5,231.3)		
4	6,193.9 (5,971.8-6,416.1)			

The three-way interaction between fish origin, year-class, and age for weight was significant ($F(2, 4{,}869) = 4.63$, $p = 0.01$). We determined that hatchery origin age-1 fish were heavier than the natural origin age-1 fish for the 2007 year-class ($t(4{,}869) = 2.22$, $p = 0.03$), the 2008 year-class ($t(4{,}869) = 2.18$, $p = 0.03$), and the 2009 year-class ($t(4{,}869) = 2.35$, $p = 0.02$). Hatchery origin age-2 fish were heavier than the natural origin age-2 fish for the 2008 year-class ($t(4{,}869) = 8.69$, $p < 0.01$). Additionally, hatchery origin age-3 fish were heavier than the natural origin age-3 fish for the 2006 year-class ($t(4{,}869) = 2.07$, $p = 0.04$) and the 2007 year-class ($t(4{,}869) = 3.06$, $p < 0.01$; Figure 14). All other fish origin, year-class, and age comparisons for average weight were similar (Figure 14).

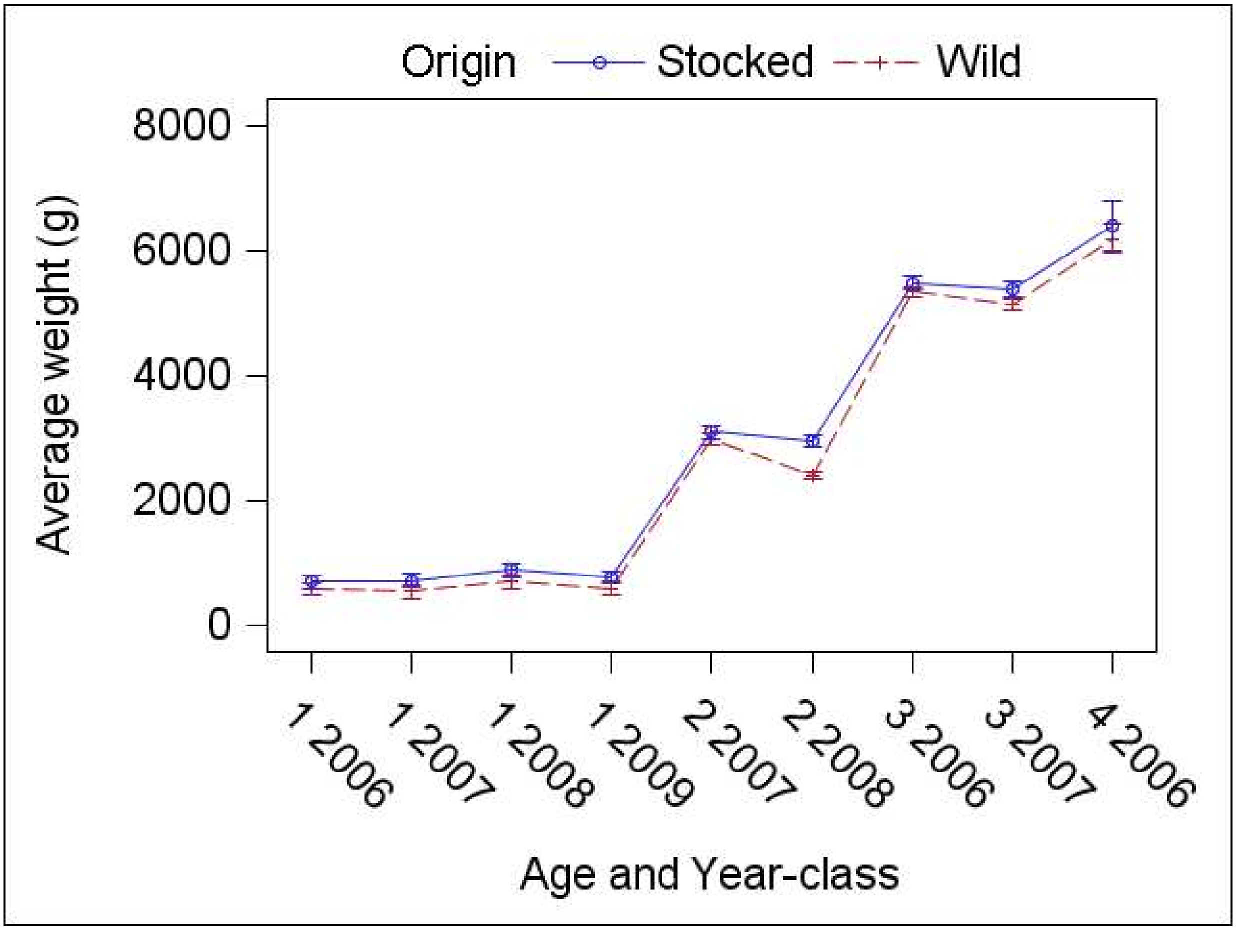

Figure 14.—Lake Michigan stocked and wild origin Chinook salmon average weight (g) by age and year-class.

Moreover, we found hatchery origin Chinook salmon weight-at-age did not have a significant year-class effect, but it did have small year-to-year variation. However, we found natural origin Chinook salmon weight-at-age did have a significant year-class effect. We determined the 2007 year-class of age-2 natural origin Chinook salmon were heavier than the 2008 year-class of age-2 natural origin fish ($t(4,869) = 9.87$, $p < 0.01$; Figure 14). We also determined the 2006 year-class of age-3 natural origin Chinook salmon were heavier than the 2007 year-class of age-3 natural origin fish ($t(4,869) = 3.26$, $p < 0.01$; Figure 14).

Estimates of Maturity-at-age

The three-way interaction between fish origin, year-class, and age for maturation-at-age was non-significant ($F(2, 1{,}021) = 0.00$, $p = 1.00$). The two-way interaction between year-class and age for maturation-at-age was also non-significant ($F(2, 1{,}030) = 2.02$, $p = 0.13$). However, a significantly larger proportion of age-2 Chinook salmon were mature from the 2008 year-class than from the 2007 year-class ($t(1{,}030) = 6.62$, $p < 0.01$; Figure 15).

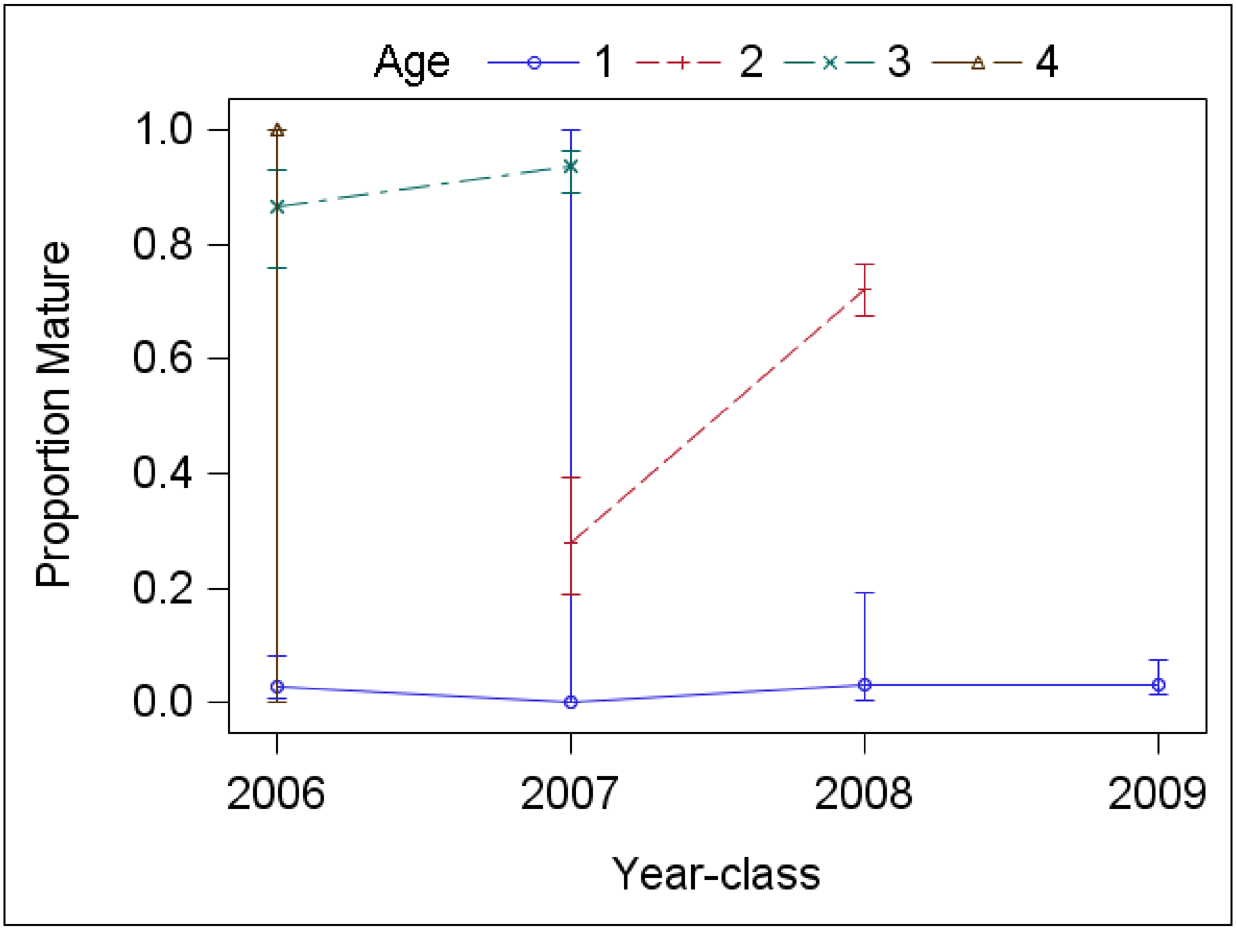

Figure 15.—Lake Michigan Chinook salmon proportions mature by year-class and age.

The three-way interaction between fish origin, sex, and age for maturation-at-age was non-significant ($F(3, 846) = 0.14$, $p = 0.94$), however, the two-way interaction between sex and age was significant ($F(3, 846) = 2.65$, $p = 0.04$). Male fish (66%) were more likely to be mature at age-2 than female fish (47%; $t(846) = 3.17$, $p < 0.01$). The proportion of mature male and female Chinook salmon were similar at age-1, age-3, and age-4 (Figure 16).

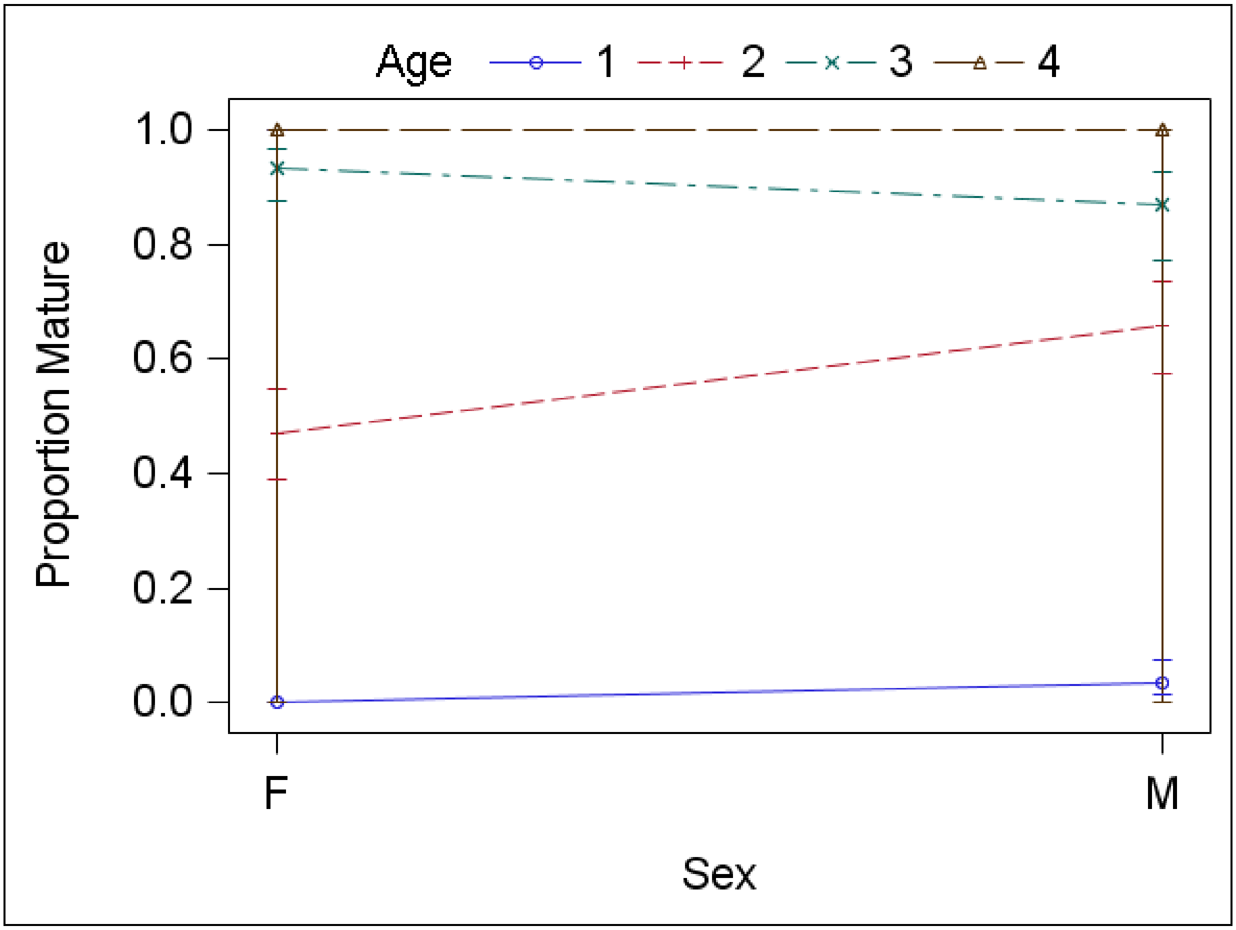

Figure 16.—Lake Michigan Chinook salmon proportion mature by fish sex (F = Female and M = Male) and age.

Additionally, we examined only the age-2 Chinook salmon from the 2008 year-class because there were significantly more mature fish for that particular cohort. The two-way interaction between fish origin and sex was non-significant ($F(1, 249) = 0.00$, $p = 0.99$; Figure 17), but the main effects of both fish origin ($F(1, 249) = 4.97$, $p = 0.03$) and sex ($F(1, 249) = 9.04$, $p < 0.01$) were significant (Figures 18 and 19). For age-2

Chinook salmon, the percentage of mature male fish (75.39%) was greater than the percentage of mature female fish (54.53%; $t(249) = 3.01$, $p < 0.01$; Figure 18) and the percentage of mature hatchery origin fish (73.08%) was greater than the percentage of mature natural origin fish (57.52%; $t(249) = 2.23$, $p = 0.03$; Figure19).

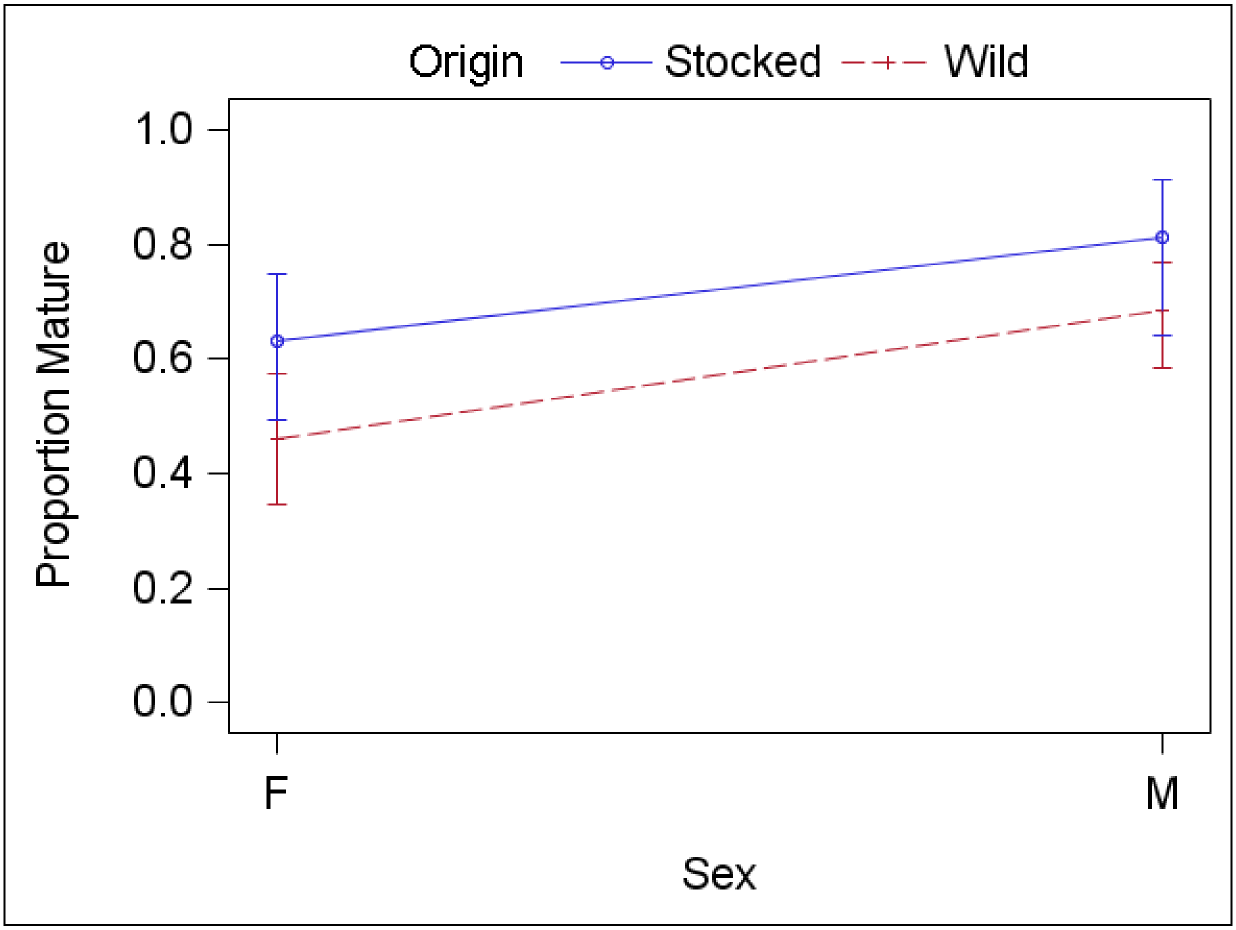

Figure 17.—Lake Michigan Chinook salmon proportions mature at age-2 by fish sex (F = Female and M = Male) and origin (2008 year-class data only).

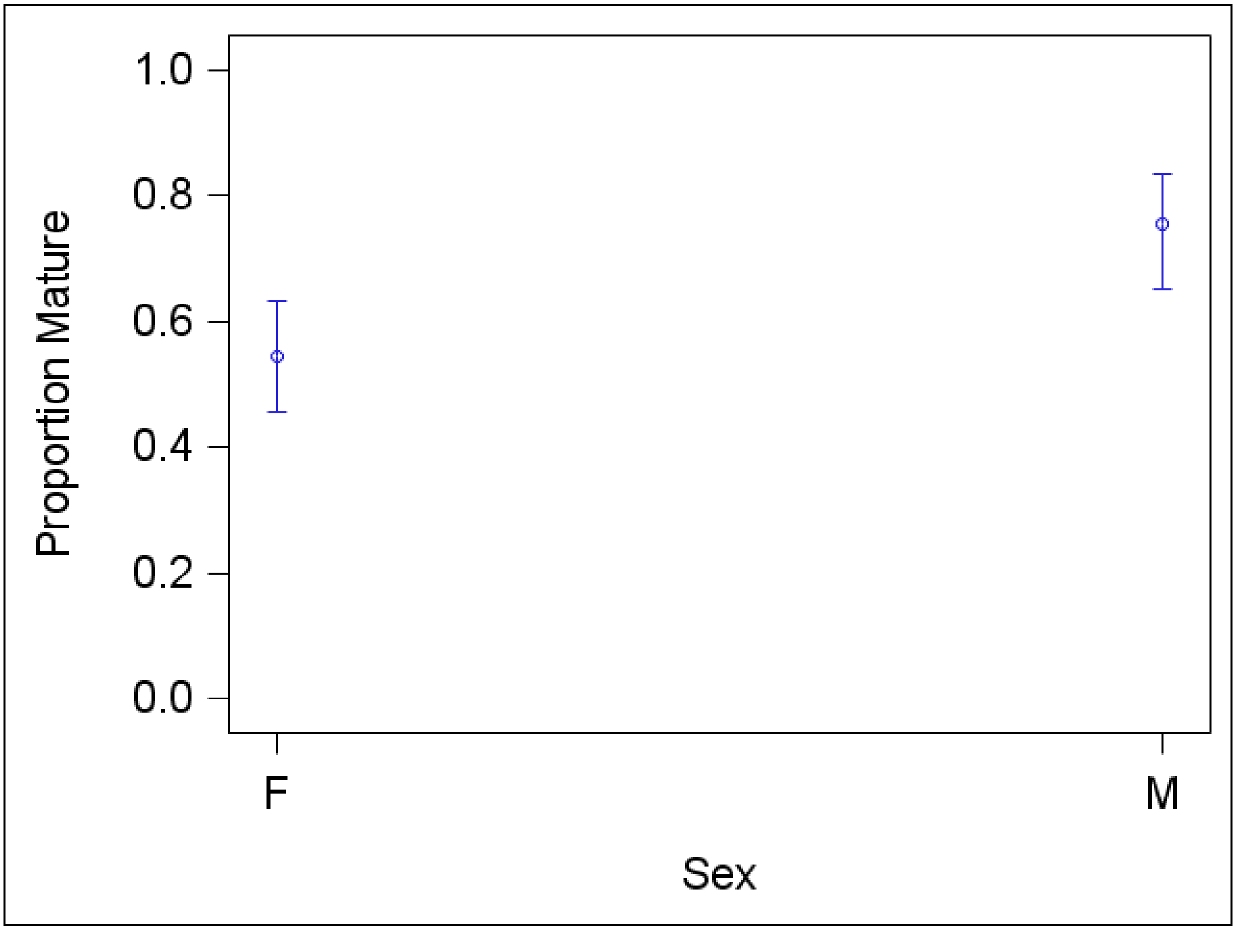

Figure 18.—Lake Michigan Chinook salmon proportions mature at age-2 by fish sex (F = Female and M = Male; 2008 year-class data only).

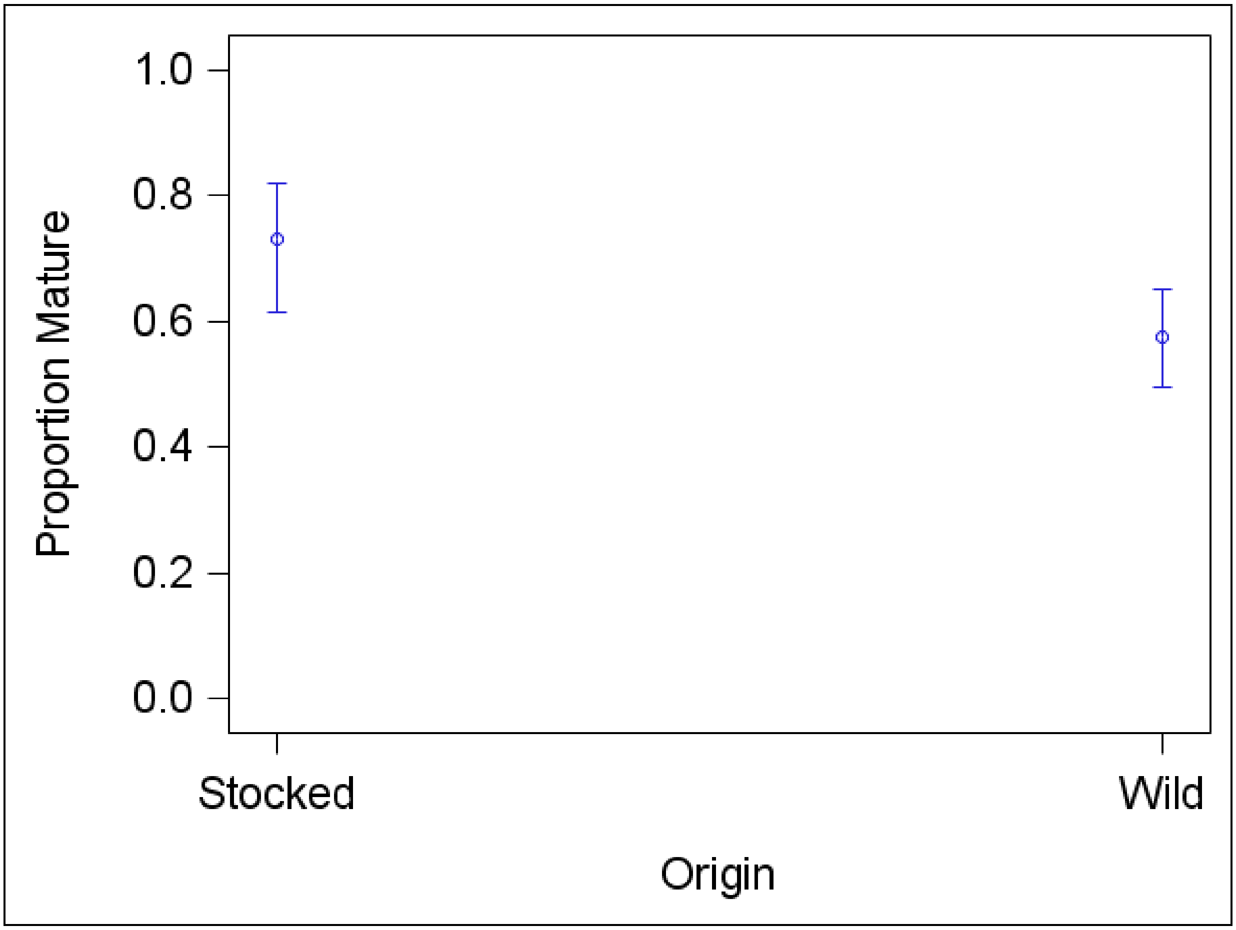

Figure 19.—Lake Michigan Chinook salmon proportions mature at age-2 by fish origin (2008 year-class data only).

DISCUSSION

OTC Mark Quality, Assimilation, and Retention

Single- and double-marked fish showed slight variation in OTC mark quality between year-classes and as the fish aged. Small changes in the OTC mark quality categories do not have management implications because the conclusion that the OTC marks were present did not change. Fortunately, poor quality OTC marks represented less than 8% of the OTC mark classifications for single- and double-marked fish. We concluded that poor OTC mark quality did not introduce significant error into our results. Our results are consistent with previous research, which demonstrated that Pacific salmon can be effectively marked by OTC feed and OTC mark retention was high (Hesse 1994; Rutherford et al. 2002; Johnson et al. 2010).

Our QAQC and error matrix results also indicated that Chinook salmon were marked successfully and consistently during our study. For the 2006 to 2009 year-classes, 92.5% of the hatchery QAQC fish had detectable OTC marks and the error matrix false negative and false positive error rates were both less than one percent. The error matrix fish were essentially a QAQC for older aged Chinook salmon and confirmed that we had an OTC marking success of nearly 100% at the time of recovery. These results were consistent with Weber and Ridgeway (1967), Hesse (1994), and Johnson et al. (2010), all of whom indicated that OTC marks were detectable after 3.5 years.

For 2009 and 2010, reader agreement on OTC mark quality categories was considered fair to good. More importantly, reader agreement on OTC mark presence and absence was excellent, which is consistent with the results of Hesse (1994) and

Johnson et al. (2010). Hesse (1994) did not report a Kappa value and Johnson et al. (2010) reported a Kappa value of 0.89. Conversely, Rutherford et al. (2002) reported OTC mark reader agreement issues.

During our study, Chinook salmon stock out deadlines caused hatchery QAQC samples to be collected within one to two weeks after the fish had been treated with OTC feed. Consistent with previous research, we determined that OTC marks can be difficult to detect immediately after the marking period because the marks are usually located on the outer edge of the vertebra and the assimilation of the OTC mark into the calcified structure (i.e., vertebrae) is not immediate. Furthermore, Johnson et al. 2010 suggested that the incidence of poor OTC marks could be reduced by increasing the minimum fish size required to initiate OTC marking from an average weight of 4 g to 5 g per fish. Previous research has documented issues with using QAQC fish and indicated that error matrix fish are more reliable (Rutherford et al. 2002 and Johnson et al. 2010). We could not agree more and recommend that future OTC studies use an age-specific classification error matrix applied to fish captured after at least one year at large, rather than a QAQC procedure for recently marked fish.

Estimates of Origin by Area, Year-class, and Age

Our hypothesis that the proportion of naturally-produced Chinook salmon in Lake Michigan would vary considerably between year-classes was not supported by our results. Our estimated lakewide proportion of age-1 natural Chinook salmon for four year-classes ranged from 53.52 to 56.92%, which was less year-to-year variation than expected. In the early 2000s, Johnson et al. (2010) also found little variation in wild recruitment for four year-classes of Chinook salmon Lake Huron, which was also not expected. Warner et al. (2008) did not find strong evidence for density-dependence in age-1 Chinook salmon growth and condition in Lake Michigan from 1992-1996 and 2001-2005, which would argue against relatively constant recruitment over time. However, our study occurred from 2006 to 2010 and Chinook salmon might have by this time reached population sizes where density dependent effects were affecting year-class strength due to saturation of available spawning habitat or the low prey population size.

Our hypothesis that southern Lake Michigan would have a higher percentage of naturally-produced Chinook salmon than northern Lake Michigan was also not supported by our results. There was no difference in the proportion of natural origin Chinook salmon between northern and southern Lake Michigan for all four age-classes.

Our hypothesis that eastern Lake Michigan would have a higher percentage of naturally-produced Chinook salmon than western Lake Michigan was supported by our results for age-1 fish, but not older aged fish. This result was interesting, but not surprising as the majority of Lake Michigan tributaries that have good quality spawning habitat are located on the eastern shoreline (Carl 1982; Carl 1984; Zafft 1992). Cloern (1976) also determined that the most suitable Wisconsin tributary for coho salmon natural reproduction did not possess the necessary physical characteristics of good quality spawning habitat. Additionally, the fact that the proportions of natural origin age-2 and older fish for Michigan and Wisconsin waters were similar has important management implications. It appears that wild Chinook salmon are well mixed into the lakewide population by age-2, which suggests that greater reliance on natural origin fish should not negatively affect the Wisconsin recreational fishery as much as might have been feared.

We determined that the proportion of naturally-produced Chinook salmon increased as the fish became older (i.e., age-effect) for the lakewide, jurisdiction, and region analyses. The proportion of naturally-produced age-1 Chinook salmon not only varied between eastern and western Lake Michigan, but varied between the four regions. Our hypothesis that southeast Lake Michigan would have the highest percentage of naturally-produced Chinook salmon was supported by our results for age-1 fish, but not older aged fish. This is not surprising because previous research found the highest levels of Chinook salmon natural reproduction for Lake Michigan occurred in the south central region between Holland and Whitehall, which is within our southeast region and was consistent with our results (Carl 1982; Elliott 1994; Hesse 1994; Johnson et al. 2005; Krueger 2010). Additionally, the proportion of naturally-produced Chinook salmon in the northeast, northwest, and southwest regions all had an age-effect, however, the southeast region did not have an age-effect. Hesse (1994) found the proportion of naturally-produced Chinook salmon in Frankfort and Ludington, MI had an age-effect, which is within our northeast region and was consistent with our results. In Grand Haven, MI Hesse (1994) found the proportion of naturally-produced Chinook salmon did not have an age-effect, which is within our southeast region and was consistent with our findings.

We now have better estimates of the contribution of natural origin Chinook in Lake Michigan and how the contributions fluctuate both spatially and temporally at different levels, however, we are still uncertain about which abiotic and biotic factors are responsible for the spatial and temporal variation. We believe that several factors may contribute to spatial and temporal variation in the contribution of natural origin Chinook salmon in Lake Michigan including: (1) migration of unmarked hatchery and natural origin Chinook salmon from Lake Huron into Lake Michigan between age-1 and age-2; (2) mixing of unmarked natural origin Chinook salmon from southeast Lake Michigan to other regions of the lake between age-1 and age-2; (3) differences in maturation patterns between natural and hatchery origin Chinook salmon; (4) differences in survival between natural and hatchery origin Chinook salmon; or (5) a combination of these factors.

Based on our results and previous research, we believe that the first two factors are more likely causing the proportion of naturally-produced Chinook salmon to increase as the fish age. First, the age-effect might have occurred because unmarked hatchery and natural origin Chinook salmon from Lake Huron were immigrating into Lake Michigan, thus causing the observed proportion of naturally-produced Chinook salmon to increase as the fish became older. Chinook salmon are well known to move great distances during their oceanic life stage in the Pacific Ocean (Healey and Groot 1987; Healey 1991). From 1991 to 2002, the MDNR found movement of Chinook salmon from Lake Huron into Lake Michigan varied between 1.8 and 27.8% based on absolute numbers of CWT recoveries. The true extent of Chinook salmon migration between the lakes is currently unknown due to biases in the CWT recapture and fishing effort.

Second, the higher incidence of natural origin Chinook salmon in the southeast region may act as a source population for the other three regions of Lake Michigan, but mixing of these different lake regions does not occur until after the fish are age-1.

Adlerstein et al. (2008) found that Chinook salmon: tend to congregate in southern Lake Michigan during winter and spring; showed a northward progression from May to July; and moved from nearshore to offshore waters during July and August.

The maturational differences between natural and hatchery origin Chinook salmon are less likely to explain the fish origin patterns we observed because they did not appear until age-2. Thus, maturational differences we observed would not affect the proportion of wild Chinook salmon until age-3 whereas the increase in the proportion of wild fish was observed at age-2.

Estimates of Size-at-age and Maturity-at-age

We observed size-at-age differences between natural and hatchery origin Chinook salmon in Lake Michigan, however, we are uncertain whether these relatively small size-at-age differences have much biological significance, or contribute to age-specific survival differences between natural and hatchery origin fish. Additionally, we observed that the size-at-age differences between natural and hatchery origin Chinook salmon decreased as fish aged. Johnson et al. (2010) suggested that age-0 hatchery-reared Chinook salmon were larger than their natural counterparts, which could decrease the predation risk (i.e., decrease mortality) for hatchery fish. Elliott (1994) indicated that the proportion of natural origin Chinook salmon was significantly higher at age-0 than age-1, suggesting that hatchery origin fish have better survival during early life stages. However, Johnson et al. (2010) and Elliott (1994) data analyses included age-0 Chinook salmon whereas our data analyses only included fish age-1 and older.

During our study, maturation differences between Chinook salmon origin and sex were only apparent at age-2. To our knowledge, no previous research on the Great

Lakes has examined maturational differences between natural and hatchery origin Chinook salmon or other salmonids. However, growth and maturational differences between natural and hatchery origin Chinook salmon have been researched in the Pacific Northwest (Larsen et al. 2004 and 2006; Shearer et al. 2000 and 2006). Larsen et al. (2006) indicated that the maturation rate and adiposity of hatchery Chinook salmon was higher than wild Chinook salmon, consistent with our findings of age-2 Chinook salmon. Chinook salmon maturation differences between natural and hatchery origin fish may affect survival rates and relative contributions to the creel. Moreover, differences in maturation rates and survival are intertwined because Chinook salmon are semelparous. Earlier maturation or lower survival of hatchery fish could cause the proportion of naturally-produced Chinook salmon to increase with age. For example, a larger proportion of male hatchery-reared Chinook salmon could mature earlier (i.e., higher mortality rate), leaving a greater proportion of natural origin fish in Lake Michigan.

Natural Reproduction

From 1969 to 1985, scientists observed that Chinook salmon populations in the Great Lakes were positively correlated with stocking and that survival appeared to be density independent (Hesse 1994; Kocik and Jones 1999; Hansen and Holey 2002). Since the mid-1980s, Chinook salmon natural reproduction in Lake Michigan has led to naturalized populations that appear to fluctuate based on natural feedbacks (i.e., abiotic and biotic factors) from lake and river conditions as opposed to salmon stocking programs. Currently, Lake Michigan Fish Community Objectives (FCO) recognize Chinook salmon as a naturalized species and recommend that natural reproduction be promoted and enhanced (Eshenroder et al. 1995; Hansen and Holey 2002; Claramunt et al. 2012). Continued research on the lakewide contribution of natural origin Chinook salmon in Lake Michigan will thus be critical to a better understanding of the predator demand and population size and age structure (Szalai and Bence 2002; Rutherford et al. 2002; Jonas et al. 2008); thereby informing better management decisions.

For the 2006 to 2009 year-classes, we estimated the number naturally-produced Chinook salmon in Lake Michigan ranged between 3,138,172 and 4,151,668 (Figure 20). Our estimates were derived similar to Hesse (1994) and assumed equal survival of hatchery and natural origin Chinook salmon to age-1. Our estimates of natural reproduction were greater than the lakewide estimates derived by Carl (1982), Keller et al. (1990), and Hesse (1994), and are similar to the lakewide estimates derived by the MDNR in the early 2000s (Figure 20). Early in the time series, fluctuations in Chinook salmon recruitment can be attributed to changes in stocking, however, recent changes have also been affected by an increase in natural reproduction. Natural reproduction has increased throughout the time series. Current estimates from our study suggest that naturally-produced age-1 Chinook salmon account for approximately 53.5 to 56.1% of the lakewide recruitment for the 2006 to 2009 year-classes.

Comparisons of our estimates of natural reproduction to previous “lakewide” natural reproduction estimates should be made with caution. Previous estimates had greater uncertainty because they were derived by extrapolating data from either stream-specific or partial lakewide OTC surveys. Additionally, our estimates of naturally-produced Chinook salmon for Lake Michigan should not be considered representative of years prior to the 2006 to 2009 year-classes because the Lake Michigan ecosystem and predator and prey populations, which may be responsible for changes in natural reproduction, are vastly different now than when the previous natural reproduction studies occurred.

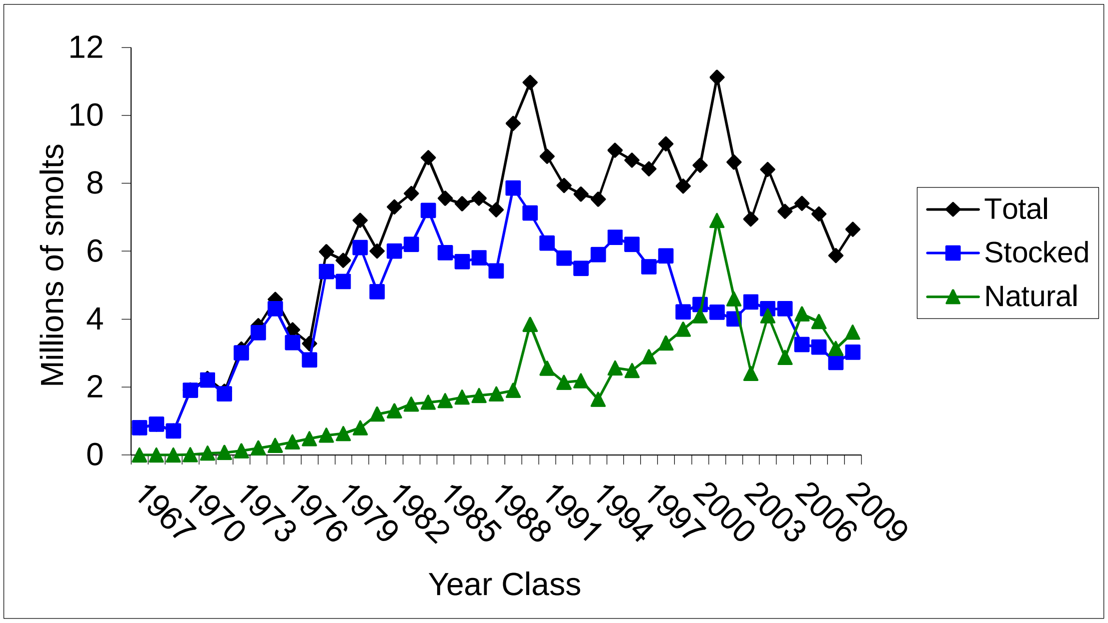

Figure 20.—Estimate of Chinook salmon recruitment in Lake Michigan for the 1967-2009 year-classes.

During our study, we assumed that Chinook salmon were well mixed during the months of April through August. We also assumed that natural and hatchery origin fish are equally susceptible to capture by tournament anglers. We relied on collecting information on Chinook salmon population dynamics from fishing tournaments, however, some tournaments were cancelled due to weather conditions and reduced the total sample size. Chinook salmon data was only collected from late April until mid August because natural and hatchery origin Chinook salmon were not considered randomly mixed after August. Data from northern Lake Michigan was underrepresented because the majority of fishing tournaments in that portion of the lake occurred in

August and September. Nevertheless, we believe that our sampling was representative of the large majority of Chinook salmon natural reproduction in Lake Michigan. Fish samples were collected from all times and locations where a substantial amount of fishing occurred and it seems unlikely that the fishery fails to target a significant component of the Chinook stocks in the lake. We can think of no reason that our assumptions of mixing and equal susceptibility to fishing for hatchery and wild fish would be violated.

We acknowledge, but did not correct for, the fact that 4.85% (157,904 of 3,252,769) of the Chinook salmon from the 2006 year-class were stocked into Lake Michigan waters by Illinois without a unique mark that could be used to identify it as a hatchery-reared fish. We ultimately decided not to correct for these unmarked fish because the percentage of natural origin Chinook salmon from the 2006 year-class at age-1 and age-3 was not statistically different from age-1 and age-3 fish from other year-classes. If these fish had 100% survival, which is unrealistic, the contribution of natural origin Chinook salmon for the 2006 year-class could be adjusted lower by 4.85% for each age-class.

Current and Future Research

The Chinook salmon OTC Project will continue through 2013. The final Chinook salmon OTC dataset will include five cohorts of age-1 fish from the 2006, 2007, 2008, 2009, and 2010 year-classes; four cohorts of age-2 fish from the 2007, 2008, 2009, and 2010 year-classes; five cohorts of age-3 fish from the 2006, 2007, 2008, 2009, and 2010 year-classes; four cohorts of age-4 fish from the 2006, 2007, 2008, and 2009 year-classes; and three cohorts of age-5 fish from the 2006, 2007, and 2008 year-classes.

In 2011, the Great Lakes CWT Mass-marking Project was initiated. This project marked all lake trout and Chinook salmon. The Great Lakes mass-marking project was funded by the Great Lakes Restoration Initiative (GLRI) and addressed the need for a long-term, multi-agency strategy for assessing natural reproduction of salmonines on a lakewide scale, which is similar to the Chinook salmon OTC Project. In addition to producing estimates of natural reproduction, the marking of specific groups of fish from each agency and hatchery with unique CWT lot codes provided the advantage to assess the following: stocking site success; stocking method success; hatchery performance; fish contribution to the creel; fish survival and maturation patterns; fish movement in general; immigration and emigration of fish between the Great Lakes, especially Lakes Michigan and Huron; and other subjects of interest (SWG 2012). Compared to the Chinook salmon OTC project, the CWT mass-marking project has less uncertainty in fish age and origin as well.

Future research should continue to examine the factors that influence Chinook salmon natural production and proportional contributions including movement of adult Chinook salmon between Lakes Huron and Michigan, mixing of natural origin Chinook salmon in Lake Michigan between age-1 and age-2, growth and survival of early life stages of natural and hatchery origin Chinook salmon, and maturation differences between natural and hatchery origin Chinook salmon. Currently, there is interest in reducing the amount of Chinook salmon stocked into Lake Michigan due to concerns about a predator-prey imbalance. Managers and stakeholders are trying to avoid a

Chinook salmon and alewife population collapse similar to the collapse that occurred in Lake Huron in the early 2000s.

Chinook salmon wild reproduction is now large enough that changes to stocking will have less of an effect on overall predator demand, compared to the perception of the significance of stocking when earlier stocking reductions were implemented. The knowledge gained from the Chinook Salmon OTC Project and this thesis research will help determine how naturally-produced Chinook salmon affects the Lake Michigan Chinook salmon population and recreational fishery and will assist Great Lakes fishery managers in making decisions regarding future salmonine stocking programs.

APPENDICES

Table A-1.—Age-1 uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by management unit and year-class. Sample sizes are shown in parentheses.

Age-1		**Year-class**			
Management Unit	**Mean Julian Date**	2006	2007	2008	2009
MM-1	202, - , - , -	67.57 (37)	-	-	-
MM-3	178, - , - , -	100.00 (1)	-	-	-
MM-5	217, 200, 205, -	60.71 (28)	64.28 (28)	50.00 (2)	-
MM-6	206, 202, 196, 188	47.54 (61)	48.78 (41)	62.79 (43)	49.25 (67)
MM-7	167, 158, 159, 156	59.29 (113)	60.16 (246)	55.90 (161)	73.17 (205)
MM-8	173, 176, 136, 132	57.45 (94)	46.15 (26)	100.00 (1)	44.11 (34)
Michigan overall	184, 166, 167, 160	57.78 (334)	58.06 (341)	57.48 (207)	64.70 (306)
WM-2	- , 208, - , 205	-	62.85 (70)	-	36.36 (33)
WM-3	200, 208, 200, 186	63.64 (66)	50.00 (22)	38.46 (26)	37.83 (37)
WM-4	203, 209, 214, 194	64.52 (31)	40.00 (25)	52.83 (53)	44.00 (25)
WM-5	209, 208, 206, 207	47.37 (152)	40.90 (88)	53.33 (180)	43.97 (166)
WM-6	200, 199, 195, 196	38.89 (18)	45.45 (11)	25.00 (28)	69.23 (13)
Wisconsin overall	206, 208, 206, 202	52.81 (267)	49.07 (216)	49.12 (287)	43.43 (274)
Illinois overall	217, 163, 234, 225	85.71 (28)	33.33 (12)	81.25 (16)	69.56 (23)
Indiana overall	- , 125, 135, 121	-	50.00 (2)	50.00 (2)	33.33 (21)
Lake Michigan overall	195, 182, 191, 180	56.92 (629)	54.11 (571)	53.51 (512)	54.48 (624)

Table A-2.—Age-2 uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by management unit and year-class. Sample sizes are shown in parentheses.

Age-2		**Year-class**			
Management Unit	**Mean Julian Date**	2006	2007	2008	2009
MM-1	- , - , - , -	-	-	-	-
MM-3	-, 210, - , -	-	100.00 (1)	-	-
MM-5	238, 191, - , -	75.00 (4)	100.00 (2)	-	-
MM-6	212, 193, 190, -	86.66 (15)	73.33 (30)	68.37 (98)	-
MM-7	182, 150, 156, -	100.00 (19)	47.46 (59)	72.22 (90)	-
MM-8	219, 132, 132, -	50.00 (4)	57.65 (85)	65.65 (131)	-
Michigan overall	200, 150, 157, -	88.09 (42)	57.62 (177)	68.34 (319)	-
WM-2	212, - , 205, -	69.23 (13)	-	64.29 (28)	-
WM-3	203, 195, 180, -	100.00 (3)	58.11 (74)	68.33 (60)	-
WM-4	210, 203, 193, -	60.00 (5)	73.02 (63)	72.22 (72)	-
WM-5	199, 205, 201, -	84.84 (99)	70.59 (119)	77.86 (131)	-
WM-6	197, 195, 195, -	76.19 (63)	60.71 (84)	73.08 (104)	-
Wisconsin overall	200, 200, 195, -	80.32 (183)	65.88 (340)	73.16 (395)	-
Illinois overall	172, 231, 224, -	87.03 (54)	61.54 (13)	73.47 (49)	-
Indiana overall	- , 119, 121, -	-	61.11 (36)	60.43 (187)	-
Lake Michigan overall	195, 180, 169, -	82.79 (279)	62.89 (566)	69.05 (950)	-

Table A-3.—Age-3 uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by management unit and year-class. Sample sizes are shown in parentheses.

Age-3		Year-class			
Management Unit	**Mean Julian Date**	2006	2007	2008	2009
MM-1	- , - , - , -	-	-	-	-
MM-3	-, - , - , -	-	-	-	-
MM-5	205, - , - , -	100.00 (5)	-	-	-
MM-6	196, 193, - , -	89.29 (28)	65.94 (138)	-	-
MM-7	150, 157, - , -	64.86 (37)	55.55 (18)	-	-
MM-8	132, 133, - , -	62.94 (143)	57.38 (61)	-	-
Michigan overall	145, 173, - , -	67.61 (213)	62.67 (217)	-	-
WM-2	- , 205, - , -	-	66.66 (12)	-	-
WM-3	192, 179, - , -	64.63 (82)	63.41 (82)	-	-
WM-4	188, 193, - , -	78.13 (32)	50.00 (34)	-	-
WM-5	205, 201, - , -	75.38 (65)	60.00 (45)	-	-
WM-6	194, 195, - , -	66.66 (111)	60.40 (101)	-	-
Wisconsin overall	195, 191, - , -	69.31 (290)	60.22 (274)	-	-
Illinois overall	224, 221, - , -	55.55 (9)	71.43 (14)	-	-
Indiana overall	116,121, - , -	61.58 (177)	65.63 (64)	-	-
Lake Michigan overall	160, 177, - , -	66.62 (689)	62.04 (569)	-	-

Table A-4.—Age-4 uncorrected proportion of natural origin Chinook salmon observed from the Lake Michigan sport fishery by management unit and year-class. Sample sizes are shown in the parentheses.

Age-4		**Year-class**			
Management Unit	**Mean Julian Date**	2006	2007	2008	2009
MM-1		-	-	-	-
MM-3		-	-	-	-
MM-5		-	-	-	-
MM-6	197, - , - , -	80.95 (21)	-	-	-
MM-7	156, - , - , -	100.00 (1)	-	-	-
MM-8	132, - , - , -	71.43 (7)	-	-	-
Michigan overall	180, - , - , -	79.31 (29)	-	-	-
WM-2	- , - , - , -	-	-	-	-
WM-3	180, - , - , -	83.33 (6)	-	-	-
WM-4	192, - , - , -	100.00 (5)	-	-	-
WM-5	202, - , - , -	85.71 (7)	-	-	-
WM-6	195, - , - , -	71.43 (28)	-	-	-
Wisconsin overall	194, - , - , -	78.26 (46)	-	-	-
Illinois overall	- , - , -, -	-	-	-	-
Indiana overall	118, - , - , -	57.14 (7)	-	-	-
Lake Michigan overall	183, - , - , -	76.83 (82)	-	-	-

Table B-1.—Lakewide model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Lakewide	year-class x age	year-class x age	F = 1.59	(2, 5,187)	0.2050
		year-class	F = 2.29	(3, 5,187)	0.0762
		age	F = 20.39	(3, 5,187)	**< 0.0001**
	year-class, age	year-class	F = 2.43	(3, 5,189)	0.0637
		age	F = 20.93	(3, 5,189)	**< 0.0001**
		LS Means - age 1 vs. age 2	t = 6.55	5,189	**< 0.0001**
		LS Means - age 1 vs. age 3	t = 5.12	5,189	**< 0.0001**
		LS Means - age 1 vs. age 4	t = 3.39	5,189	**0.0039**
		LS Means - age 2 vs. age 3	t = 1.17	5,189	0.6444
		LS Means - age 2 vs. age 4	t = 1.41	5,189	0.4931
		LS Means - age 3 vs. age 4	t = 1.88	5,189	0.2376

Table B-2.—Jurisdiction model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Jurisdictions: IL vs. IN vs. MM vs. WM	state x year-class x age	state x year-class x age	*F* = 1.83	(5, 5,158)	0.1027
		state x year-class	*F* = 1.39	(9, 5,158)	0.1861
		state x age	*F* = 2.16	(8, 5,158)	**0.0271**
	state x year-class, state x age	state x year-class	*F* = 1.64	(9, 5,165)	0.0988
		state x age	*F* = 2.27	(8, 5,165)	**0.0199**
		LS Means - IL - age 1 vs. age 2	*t* = 0.13	5,165	0.9910
		LS Means - IL - age 1 vs. age 3	*t* = 0.01	5,165	0.9999
		LS Means - IL - age 2 vs. age 3	*t* = 0.09	5,165	0.9956
		LS Means - IN - age 1 vs. age 2	*t* = 0.43	5,165	0.9733
		LS Means - IN - age 1 vs. age 3	*t* = 0.60	5,165	0.9313
		LS Means - IN - age 1 vs. age 4	*t* = 0.34	5,165	0.9861
		LS Means - IN - age 2 vs. age 3	*t* = 0.46	5,165	0.9683
		LS Means - IN - age 2 vs. age 4	*t* = 0.01	5,165	1.0000
		LS Means - IN - age 3 vs. age 4	*t* = 0.24	5,165	0.9954
		LS Means - MM - age 1 vs. age 2	*t* = 1.86	5,165	0.2447
		LS Means - MM - age 1 vs. age 3	*t* = 2.75	5,165	**0.0309**
		LS Means - MM - age 1 vs. age 4	*t* = 2.13	5,165	0.1422
		LS Means - MM - age 2 vs. age 3	*t* = 0.63	5,165	0.9236
		LS Means - MM - age 2 vs. age 4	*t* = 1.57	5,165	0.3979
		LS Means - MM - age 3 vs. age 4	*t* = 1.39	5,165	0.5072
		LS Means - WM - age 1 vs. age 2	*t* = 7.82	5,165	**< 0.0001**
		LS Means - WM - age 1 vs. age 3	*t* = 5.17	5,165	**< 0.0001**
		LS Means - WM - age 1 vs. age 4	*t* = 3.04	5,165	**0.0128**
		LS Means - WM - age 2 vs. age 3	*t* = 1.98	5,165	0.1950
		LS Means - WM - age 2 vs. age 4	*t* = 0.60	5,165	0.9323
		LS Means - WM - age 3 vs. age 4	*t* = 1.35	5,165	0.5298

Table B-3.—Jurisdiction model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Jurisdictions: MM vs. WM	state x year-class x age	state x year-class x age	*F* = 0.09	(2, 4,514)	0.9118
		state x year-class	*F* = 3.16	(3, 4,514)	**0.0236**
		state x age	*F* = 4.73	(3, 4,514)	**0.0027**
	state x year-class, state x age	state x year-class	*F* = 3.07	(3, 4,518)	**0.0268**
		state x age	*F* = 4.96	(3, 4,518)	**0.0019**
		LS Means - MM age 1 vs. WM age 1	*t* = 5.36	4,518	**< 0.0001**
		LS Means - MM age 2 vs. WM age 2	*t* = 1.32	4,518	0.1861
		LS Means - MM age 3 vs. WM age 3	*t* = 1.18	4,518	0.2372
		LS Means - MM age 4 vs. WM age 4	*t* = 0.56	4,518	0.5746

Table B-4.—Region model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Two-regions: North vs. South	region x year-class x age	region x year-class x age	*F* = 0.36	(2, 5,176)	0.6986
		region x age	*F* = 0.30	(4, 5,176)	0.8754
	region x year-class, region x age	region x age	*F* = 0.35	(3, 5,178)	0.7879
		region	*F* = 0.23	(1, 5,178)	0.6325
		age	*F* = 19.04	(3, 5,178)	**< 0.0001**
		LS Means - North - age 1 vs. age 2	*t* = 4.02	5,178	**0.0003**
		LS Means - North - age 1 vs. age 3	*t* = 3.24	5,178	**0.0066**
		LS Means - South - age 1 vs. age 2	*t* = 5.32	5,178	**< 0.0001**
		LS Means - South - age 1 vs. age 3	*t* = 4.03	5,178	**0.0003**

Table B-5.—Region model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Four-regions: NE vs. NW vs. SE vs. SW	region x year-class x age	region x year-class x age	F = 1.91	(6, 5,156)	0.0758
		region x age	F = 3.76	(9, 5,156)	**0.0001**
	region x year-class, region x age	region x age	F = 3.40	(9, 5,164)	**0.0004**
		LS Means - NE - age 1 vs. age 2	t = 3.10	5,176	**0.0104**
		LS Means - NE - age 1 vs. age 3	t = 3.51	5,176	**0.0026**
		LS Means - NW - age 1 vs. age 2	t = 3.73	5,176	**0.0011**
		LS Means - NW - age 1 vs. age 3	t = 2.66	5,176	**0.0389**
		LS Means - SW - age 1 vs. age 2	t = 7.65	5,176	**< 0.0001**
		LS Means - SW - age 1 vs. age 3	t = 4.97	5,176	**< 0.0001**
		LS Means - SW - age 1 vs. age 4	t = 2.77	5,176	**0.0287**
		LS Means - SE age 1 vs. SW age 1	t = 4.48	5,176	**< 0.0001**
		LS Means - SE age 2 vs. SW age 2	t = 3.35	5,176	**0.0045**

Table B-6.—Length-at-age model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Length-at-age	origin x year-class x age	origin x year-class x age	*F* = 2.74	(2, 5,150)	**0.0648**
		origin x age	*F* = 7.96	(3, 5,150)	**< 0.0001**
		LS Means - 2006 - stocked age 1 vs. wild age 1	*t* = 4.30	5,150	**< 0.0001**
		LS Means - 2007 - stocked age 1 vs. wild age 1	*t* = 6.14	5,150	**< 0.0001**
		LS Means - 2008 - stocked age 1 vs. wild age 1	*t* = 6.33	5,150	**< 0.0001**
		LS Means - 2009 - stocked age 1 vs. wild age 1	*t* = 8.55	5,150	**< 0.0001**
		LS Means - 2008 - stocked age 2 vs. wild age 2	*t* = 7.03	5,150	**< 0.0001**
	origin x year-class, origin x age	origin x year-class	*F* = 7.74	(3, 5,154)	**< 0.0001**
		origin x age	*F* = 7.03	(3, 5,154)	**0.0001**
		LS Means - stocked age 1 vs. wild age 1	*t* = 12.66	5,154	**< 0.0001**
		LS Means - stocked age 2 vs. wild age 2	*t* = 4.32	5,154	**< 0.0001**
		LS Means - stocked age 3 vs. wild age 3	*t* = 2.90	5,154	**0.0037**
		LS Means - stocked age 4 vs. wild age 4	*t* = 0.91	5,154	0.3616

Table B-7.—Weight-at-age model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Weight-at-age	origin x year-class x age	origin x year-class x age	*F* = 4.63	(2, 4,869)	**0.0098**
		LS Means - 2007 - stocked age 1 vs. wild age 1	*t* = 2.22	4,869	**0.0263**
		LS Means - 2008 - stocked age 1 vs. wild age 1	*t* = 2.18	4,869	**0.0293**
		LS Means - 2009 - stocked age 1 vs. wild age 1	*t* = 2.35	4,869	**0.0187**
		LS Means - 2008 - stocked age 2 vs. wild age 2	*t* = 8.69	4,869	**< 0.0001**
		LS Means - 2006 - stocked age 3 vs. wild age 3	*t* = 2.07	4,869	**0.0387**
		LS Means - 2007 - stocked age 3 vs. wild age 3	*t* = 3.06	4,869	**0.0022**
		LS Means - wild age 2 - 2007 vs. 2008	*t* = 9.87	4,869	**< 0.0001**
		LS Means - wild age 3 - 2006 vs. 2007	*t* = 3.26	4,869	**0.0011**

Table B-8.—Maturity-at-age model terms and statistical results. Significant p-values in bold.

Hypothesis	Model Terms	Results	Test Statistics	DF	P-value
Maturity-at-age	origin x year-class x age	origin x year-class x age	*F* = 0.00	(2, 1,021)	0.9991
	year-class x age	year-class x age	*F* = 2.02	(2, 1,030)	0.1336
		LS Means - age 2 - 2007 vs. 2008	*t* = 6.62	1,030	**< 0.0001**
	origin x sex x age	origin x sex x age	*F* = 0.14	(3, 846)	0.9365
		sex x age	*F* = 2.65	(3, 846)	**0.0400**
		LS Means - age 2 - male vs. female	*t* = 3.17	846	**0.0016**
	origin x sex	origin x sex	*F* = 0.00	(1, 249)	0.9942
		origin	*F* = 4.97	(1, 249)	**0.0267**
		sex	*F* = 9.04	(1, 249)	**0.0029**
		LS Means - 2008 age 2 - stocked vs. wild	*t* = 2.23	249	**0.0267**
		LS Means - 2008 age 2 - male vs. female	*t* = 3.01	249	**0.0029**

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