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Length-at-age and Size-Selective Mortality of the Western Basin Lake Erie Walleye
(*Sander vitreus*) Population, 2000-2008

by
Emily Crisovan

A Thesis

Submitted to the Faculty of Graduate Studies

through Biological Sciences

in Partial Fulfillment of the Requirements for

the Degree of Master of Science at the

University of Windsor

Windsor, Ontario, Canada

2011

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Length-at-age and Size-Selective Mortality of the Western Basin Lake Erie Walleye
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AUTHOR'S DECLARATION OF ORIGINALITY

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ABSTRACT

Size-selective mortality is common in systems where selective harvesting targets a specific size- or age-class. In general, commercial and recreational fisheries selectively remove the largest and fastest growing individuals, which may have evolutionary consequences. My goals were to examine length-at-age patterns, age at first and full recruitment to the fishery, and to determine if size-selective mortality existed in a commercially and recreationally fished population of walleye in Lake Erie of the Laurentian Great Lakes between 2000 and 2008. Mean fork length-at-age was found to increase from west to east within Lake Erie for age 2 and 3 walleye. However, mean fork-length at age 1 was not statistically different among sampling areas. Walleye first recruited to the fishery at age 1 and were not fully recruited by age 3. Smaller (slower growing) individuals were found to disproportionately survive to older ages than faster-growing fish, indicating that size-selective mortality of larger (faster growing) fish occurred. Size-selective mortality will likely have a negative effect on morphological (i.e., body size) and life history traits.

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CHAPTER 1: GENERAL INTRODUCTION

Many factors including, but not limited to, environmental changes, food resources and exploitation, can alter a fish population's structure (Weatherly and Gill 1987).

Therefore, it is essential to study and understand the size and age structure to enable proper population management. Using the western basin Lake Erie walleye population as an example, this thesis investigates fish growth patterns and estimates size-selective mortality through a scale back-calculation study.

Size-selective mortality occurs when mortality rates differ among fish of the same species and age-class due to differences in body size (Ricker 1969). In a population, this effect can occur naturally (i.e., through predation or overwinter mortality) or be the result of fishing activities using fishing gears that select fish of different size-classes (Ricker 1969). In general, it is believed that large and fast growing fish are more competitive for resources, are more tolerant of environmental extremes and thus have a survival advantage over small and slower growing fish during their early life stages (Sogard 1997). However, in an exploited fish population, larger individuals are more vulnerable to size-selective fishing gears, such as gillnets and trapnets, and thus experience higher mortality rates than small fish during the recruitment phase (Ricker 1969). In fish ecology, recruitment can be defined as the number of individuals in a year class that live to reach a reproductive size, a harvestable size, a specific age or size, or when they become vulnerable to certain sampling gear (Willis and Murphy 1996). In this thesis, recruitment refers to the process where fish of a year class become vulnerable to fishing gears (Ricker 1969).

Size-selective mortality changes the fish population's mean length-at-age, and such changes depend on fish sizes that are targeted by fisheries (Ricker 1969). For example, size-selective mortality can result in a progressively decreased mean length of a year class of fish at a particular age (e.g., age 1) measured at a young age (e.g., age 2 or 3) compared to a fish measured at an old age (e.g., age 4 or 5) (Ricker 1969). Further, if size-selective mortality occurs at age 1, where the large individuals are targeted and harvested by fishing gears, then the fish that have survived to be captured at older ages would have a larger back-calculated length at age 1 than the back-calculated length at age 1 of fish captured at age 5 because the larger individuals are being removed sooner, leaving smaller fish in the population.

Since size-selective mortality can be a result of high fishing mortality, fish populations that are selectively harvested are likely at risk of size-selective mortality. Over time, excessive fishing efforts can reduce the mean size-at-age of the fish observed in the population (Weatherly and Gill 1987). Various strategies are used by fisheries managers to prevent over-exploitation of a fish species. Commercial fishing activities are limited in the types of fishing gears, intensity of fishing effort, and harvest quotas, whereas recreational anglers are limited in the length of fish they are allowed to keep and by daily harvest limits (Kohler and Hubert 1993 in Vandergoot et al. 2010).

The walleye population in the western basin of Lake Erie is considered to be an ideal model for studying size-selective mortality. In this study, I applied a back-calculation technique using walleye scales collected from three sub-basins (western basin, west-central basin and east-central basin) of Lake Erie 1) to identify the patterns of the length frequency and growth differences of walleye among the sub-basins and

year-classes, 2) to investigate the age at the first and full recruitment, and 3) to estimate size selective mortality rate and selection intensity.

The walleye (*Sander vitreus*) is an economically and ecologically important fish species in Lake Erie and in other mesotrophic Great Lakes systems. Walleyes of the western basin of Lake Erie were commercially harvested as early as 1815 (Regier et al. 1969). After peak harvests in 1956 and 1957, the population collapsed and harvests sharply decreased in subsequent years (Hatch et al. 1987). The fishery was closed in 1970 because of high tissue mercury content (Vandergoot et al. 2010). When the mercury ban was lifted in 1973, recreational fisheries were reopened in Ontario, Michigan and Ohio and commercial fishing resumed in 1976 in Canadian waters (Cowan and Paine 1997). However, the quota of walleye permitted to be caught in US waters of Lake Erie was allocated almost entirely to recreational angling (Hatch et al. 1987). Regulations were established to prevent the over-exploitation of the walleye population, such as the development of individual quotas for each commercial operation (Cowan and Paine 1997). The Canadian walleye commercial fishery in Lake Erie uses graded-mesh gillnets to harvest fish. Ontario requires that the fishery use gillnets with a mesh size of at least 89 mm stretched; this mesh size is expected to mainly target walleye with a total length of 406 to 533 mm, which have the highest market value (Vandergoot et al. 2010). By consistently targeting these relatively large walleye, the commercial fishery may be artificially selecting for smaller, slower growing walleye in the lake population.

In addition to being economically valuable, walleye also play an important role in the Lake Erie ecosystem. As a top predator, walleye can influence the trophic structure of north temperate fish communities in mesotrophic lakes through top-down cascading

effects (Ryder and Kerr 1978; McQueen et al. 1986; Carpenter and Kitchell 1988; Ryan et al. 1999). Therefore, it is essential to understand the survivorship, age and size structure of the population, and the potential impact of fishing activities on the dynamics of the walleye population in the western basin of Lake Erie.

Despite the presence of multiple walleye spawning stocks in Lake Erie, each spawning population has not yet been clearly identified. In general, walleyes in Lake Erie are grouped into two main spawning stocks - the western basin stock and the eastern basin stock (Vandergoot et al. 2010). The western basin walleye population refers to walleye that spawn in the western basin of Lake Erie and occupy the western and central basins of the lake during summer and fall (Vandergoot et al. 2010). Several studies have shown that western basin walleyes travel into the central and eastern basins of Lake Erie as well as into Lake St. Clair and Lake Huron (Wolfert 1963; Todd and Haas 1993; Wang et al. 2007). Western basin Lake Erie walleyes are estimated to make up approximately 95% of the lakewide commercial harvest (WTG 2001). This thesis will focus on the western basin walleye stock.

It is crucial to understand the dynamics of the western basin walleye population because the area is heavily fished, and thus size-selective mortality has potential to greatly influence the population. The specific goals of this research were to (1) study the fork length-at-age of the western basin Lake Erie walleye population and compare fork length-at-age sub-basins where the fish were sampled; (2) determine if this population experiences size-selective mortality; (3) if size-selective mortality occurs, determine the age at which walleye are first affected by the size-selective mortality, and (4) estimate the intensity of the selection. The following postulates were tested: 1) those large or fast

growing walleyes of the western basin stock tend to disperse at young ages and farther to the central and east basin. This can be evaluated by examining the differences in mean length of walleye sampled from three areas of Lake Erie: the western basin, the west-central sub-basin and east-central sub-basin. 2) Since the western basin Lake Erie walleye population is heavily commercially and recreationally fished, this population experiences size-selective mortality, where walleye have smaller back-calculated fork lengths at older ages (e.g., age 5) than at younger ages (e.g., age 2 or 3). Tests of these hypotheses are organized into two chapters: Chapter 2 describes the fork length and growth of the western basin walleye sampled from the three sub-basins and Chapter 3 focuses on size-selective mortality of the western basin walleye population. This study provides an improved understanding of the size and age structure of the walleye population in Lake Erie and how fishing pressure may be affecting fish population dynamics.

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CHAPTER 2: EXAMINATION OF FORK LENGTH OF WESTERN BASIN WALLEYE FROM THREE SAMPLING SUB-BASINS WITHIN LAKE ERIE

Introduction

The walleye of the western basin of Lake Erie is an important fish species because of its economic and ecological roles. In order to understand the size-specific dispersal behavior and help to establish a fisheries management plan, it is important to study the size-at-age of western basin walleye along their main annual migration route—west to the east in Lake Erie (Wang et al. 2007).

“Growth” is change in size of an individual, measured by an increase in weight or length of an individual fish (Weatherly and Gill 1987; Willis and Murphy 1996) per unit time. In this thesis, growth was measured as an increase in fork length of an individual fish from one year to the next. Many factors play a role in shaping walleye growth patterns, such as lake productivity, water temperature, resource quality and abundance, and population density (Colby et al. 1979 in Hartman 2009). These abiotic and biotic factors cause members of the Percidae family to exhibit high variability in growth rates, which can be observed among populations or among individuals within the same cohort (Craig 2000). Since growth is highly variable and dependent on so many environmental factors, mean length-at-age of walleyes will likely differ among sampling areas and year-classes within Lake Erie, where temperature and resource availability and quality differ. For instance, the warm, shallow western basin provides suitable spawning and nursery habitat (Regier et al. 1979), whereas the deeper central and east basins provide cooler summer water temperatures that are more suitable for growth of larger walleye and likely contain higher abundances of forage fish (Kershner et al. 1999; Wang et al. 2007).

The results of several tagging and genetic studies suggest that Lake Erie has multiple walleye stocks. However, the data are inconclusive and too variable to permit definitive identification of individual stocks. In general, walleye have been grouped into two main, broadly distinctive stocks: the western basin and eastern basin stocks (Wolfert 1963; Todd and Haas 1993; Vandergoot et al. 2010). Many studies have described the movement of walleye within Lake Erie, as well as their travel through connecting channels to other waters, such as Lake St. Clair and Lake Huron (Ferguson 1957 in Wolfert 1963; Wolfert 1963; Ferguson and Derksen 1971; Todd and Haas 1993; Wang et al. 2007). Wolfert (1963) found that yearling walleye captured, tagged and released along the southern shore of the western basin of Lake Erie tended to move north or further westward into the western basin. Some of the tagged fish were even recaptured in the St. Clair River, Lake St. Clair, Detroit River and Lake Huron. However, there was little evidence showing the movement of yearling walleye towards the east end of Lake Erie (Wolfert 1963).

Tagging studies involving walleye mostly age 2 and older found that walleye tended to move towards the east end of Lake Erie (Ferguson 1957 in Wolfert 1963; Wang et al. 2007). Wang et al. (2007) found that western basin walleye started to move eastward to the central and eastern basins during the spring and summer. The motivation behind this migration was proposed to be a result of searching for physiologically more suitable (cool) water temperatures during the summer (Wang et al. 2007); the cooler central and eastern basins may provide a refuge from warm western basin conditions. Optimal water temperatures for growth of large walleye range from 20 to 23° C (Coutant 1977). In the western basin these temperatures are often exceeded in the summer

(Kershner et al. 1999). Additionally, walleye recaptured in the western basin of Lake Erie tended to be smaller than walleye recaptured in the central or eastern basins (Wang et al. 2007) possibly due to the thermal stress imposed by the western basin's unfavorable warm water conditions during the summer. These studies suggest that east-bound walleye are usually fish age 2 and older and are also larger than the non-migrating western basin walleye residents (Wolfert 1963; Wang et al. 2007).

This study compares the back-calculated fork length-at-age of the western basin walleye population captured in three areas of Lake Erie: the west basin, west-central sub-basin and east-central sub-basin. The objectives were to test:

- 1) if the western basin Lake Erie walleye population had different mean back-calculated fork length-at-ages 1, 2, and 3 among sub-basin of residency (capture) and

- 2) if the western basin Lake Erie walleye population's mean back-calculated fork lengths differed among year classes (2000, 2001, 2002, and 2003).

Since larger and faster-growing walleye are postulated to move eastward in Lake Erie (Wang et al. 2007), I expected to find differences in fork length-at-age among sub-basins such that mean fork length of walleye of western basin origin increases from west to east within the three sampling areas of the lake. Given that percid growth is extremely variable (Craig 2000), I expected to find differences in mean fork length-at-age among year-classes (2000, 2001, 2002, and 2003).

Materials and Methods

Study Area

All walleye samples used in this study were collected from Lake Erie through a partnership survey program (Great Lakes Fishery Commission, Lake Erie Committee Partnership Index Gillnetting Program unpubl.; Lake Erie management unit and the

Ontario Commercial Fisheries Association 2006). Lake Erie is the southernmost, shallowest, warmest, and most exploited of the five Great Lakes (Schertzer 1999; Rasul et al. 1999). Lake Erie is composed of three discrete basins: western, central and eastern basins (Figure 2.1). The three basins each have distinctive limnological characteristics and temperature regimes. The western basin, separated from the central basin by a series of rocky islands is the smallest, shallowest, and warmest of the basins (Bolsenga and Herdendorf 1993; Schertzer 1999). Walleye are the predominant predatory fish in the western basin (Schertzer 1999; Rasul et al. 1999). The central basin has the largest surface area of the three basins and has a flat bottom, whereas the eastern basin is the coolest and deepest of the three basins (Schertzer 1999). Both the central and eastern basins are stratified. Thus surface temperatures and bottom temperatures differ, whereas the western basin is not stratified and has a uniform temperature throughout (Schertzer et al. 1987; Bolsenga and Herdendorf 1993). Summer surface water temperatures are similar over the lake. However, near-bottom water temperatures vary among the basins (Schertzer et al. 1987; Bolsenga and Herdendorf 1993). Table 2.1 summarizes the surface area, mean depth, maximum depth, mean water temperature (1967-1982), and mean near-bottom temperature for each basin.

Collection of walleye and scales

All walleye scales used in this study were collected from annual partnership fish community surveys by the Ontario Ministry of Natural Resources and the Ontario Commercial Fisherman Association in Lake Erie (Great Lakes Fishery Commission, Lake Erie Committee Partnership Index Gillnetting Program unpubl.; Lake Erie management unit and the Ontario Commercial Fisheries Association 2006). Only samples from Canadian waters of the western and central basins were used for this study

in order to reduce the influence of the eastern basin walleye stock. The central basin was further divided into the west-central sub-basin and the east-central sub-basin, which resulted in three sampling areas for this study: the western basin, west-central sub-basin and east-central sub-basin (Figure 2.1). Fish were sampled annually within these basins for at least nine consecutive years. Scales collected from fish captured between 2000 and 2008 were used in this study, representing cohorts that were spawned in four calendar years: 2000-2003. The western basin was sampled in September, west-central sub-basin in September and October and east-central sub-basin in October and November.

Walleye were captured in graded monofilament gillnets measuring 381 m long by 1.8 m deep. The gillnets consisted of 14 different mesh sizes ranging from 32 to 152 mm (stretched) to ensure a representative catch of fish of all sizes of most age classes. The nets were either suspended in the water or placed along the bottom of the basins. The suspended gillnets were suspended at a depth of 1.8 m below the surface in the western basin and 5, 11, or 17 m deep in the west-central and east-central basins (Great Lakes Fishery Commission, Lake Erie Committee Partnership Index Gillnetting Program unpubl.; Lake Erie management unit and the Ontario Commercial Fisheries Association 2006). Upon capture, fork length (the distance from the tip of the snout to the fork in the caudal fin), was measured to the nearest mm, and mass was measured to the nearest g. At least 10 scales per fish were taken from below the lateral line near the tip of the left pectoral fin when pressed flat (Lake Erie management unit and the Ontario Commercial Fisheries Association 2006) and placed into individually labeled envelopes. The archived scales were pressed into acetate slides and the impressions were read using a microfiche projector to estimate walleye age.

Age estimation and measurement of walleye scales

In this study I have only included walleye age 0 to age 5 because the accuracy of aging fish using their scales decreases as the fish gets older (Craig 2000). Borkholder and Edwards (2001) found that walleye ages read from scales and dorsal fin spines agreed until the age of 5; thereafter scales tended to be less reliable than fin spines, and scale-based ages were likely underestimated.

Preliminary aging of the walleye scale samples had previously been performed by the Ontario Ministry of Natural Resources staff. On the basis of the preliminary aging, 30 samples from each age-group (age 0 to 5) for each year-class (2000-2003) of each area were randomly selected for the study (Table 2.2). In instances where fewer than 30 samples were available, all available samples were used (Table 2.2). I examined the scale impressions under a microfiche projector at 40X magnification and aged them a second time. Regenerated scales (the scales that have been lost from the fish due to injury, scratching or other reasons and have grown back without earlier circuli and/or annuli), or the scales with unclear foci and/or annuli were not used in this study because they could not be aged accurately. Ages were estimated by counting the number of annuli on the scale along the anterior-posterior axis. The closely spaced circuli was considered an annulus and was assumed to correspond with the end of the winter growth period (DeVries and Frie 1996). If first and second age estimations disagreed, scales were discarded from the study. For each sample, a projected image of the scale focus (center of the scale), each annulus and the scale margin (edge of the scale) were recorded on a strip of plastic transparency approximately 2.5 cm wide using a permanent marker. A total of 912 samples was examined in this study.

The distances recorded on the transparency strips were digitized using a SummaSketch II professional digitizer. To measure the distance from the scale focus to each annulus, a program was developed using Microsoft Visual Basic. These distances were used to estimate each individual walleye's fork length at each earlier age.

Walleye body-scale relationship

To accurately estimate length-at-age of individual walleye through back-calculation, it was essential to establish the relationship between fork length and scale radius at capture for the population. Walleye body length and scale radius do not grow in direct proportion to one another; body length increases faster than scale radius (Klumb et al. 1999). Consequently, fork length and scale radius were logarithmically transformed and a non-linear regression equation was derived for this study.

To determine if back-calculations should be performed using area-specific relationships or if one body-scale relationship for all areas would be adequate, body-scale relationships were estimated for age 0 to age 5 walleye caught in each sampling region. A total of 399 walleye scales were included for the western basin, 296 for the west-central basin and 217 for the east-central basin. A second-order polynomial equation was used to model the body-scale relationship for each area (Zhao 2005). Overlap of the 95% confidence intervals of the area specific body-scale relationships indicated that a single standard body-scale relationship for all samples collected from Lake Erie would be acceptable. Therefore, all scale samples (912 total) from the three sampling areas were pooled together to establish a single body-scale relationship. With the exception of age 0 walleye, all fish used to create the body-scale relationship were also used in the back-calculation study. The relationship was used to back-calculate the fork lengths of each fish described in the next section.

Back-calculation of fork length-at-age

Estimating fish fork lengths at age requires the use of a back-calculation equation that calculates previous body length from scale radius. This procedure relies on the correlation between body length and scale length (Whitney and Carlander 1956). A common back-calculation technique is based on the scale-proportional hypothesis, which states that the ratio of the scale radius at one age to that at another age is a function of the ratio of the body lengths at the two ages for an individual fish (Francis 1990). To determine the body length to scale radius relationship of walleye, a regression of scale length on body length was applied in this study. The following procedure was used to back-calculate fork lengths at ages (annuli). The regression equation describing the relationship between fork length (FL) and scale radius (SR) is the second order polynomial, as follows,

$$\log(\text{SR}) = a*(\log(\text{FL}))^2 + b*\log(\text{FL}) + c$$

therefore, in conjunction with the scale proportional hypothesis ($(\text{SR}/\text{SR}_n) = f(\text{FL}/\text{FL}_n)$), where SR is scale radius at capture, SR_n is the scale radius at age n, FL is the fork length at capture, FL_n is the fork length at age n, and *f* indicates a function:

$$\log(\text{SR}) - \log(\text{SR}_n) = (a*(\log(\text{FL}))^2 + b*\log(\text{FL})) - (a*(\log(\text{FL}_n))^2 + b*\log(\text{FL}_n))$$

the equation was then simplified and set to zero:

$$0 = a*(\log(\text{FL}_n))^2 + b*\log(\text{FL}_n) + d$$

where $d = (\log(\text{SR}) - \log(\text{SR}_n)) - (a*(\log(\text{FL}))^2 + b*\log(\text{FL}))$.

The fork length at age n (FL_n) for each individual walleye was calculated by solving the above quadratic equation and taking the anti-log of the positive solution. The fork length at ages 1, 2, and 3 were estimated using the above described back-calculation procedure

for all individual walleye samples (ages 1 to 5) from the three areas (western, west-central and east-central).

Statistical Analysis

A multivariate analysis of variance (MANOVA) was used (Statistica 7.0, StatSoft, Inc.) to test for the presence of significant differences in walleye back-calculated fork length at ages 1, 2, and 3 among the areas and year classes. Additionally, a planned comparison analysis was performed to identify specific differences in walleye fork length-at-age at ages 1, 2 and 3 among the three sampling areas. Two contrasts were used for this comparison: contrast 1 compared the back-calculated fork lengths of walleye captured in the western sub-basin to walleye captured in the west-central and east-central basins; contrast 2 compared the back-calculated fork lengths of walleye captured in the west-central sub-basin to walleye captured in the east-central sub-basin.

A Tukey post-hoc pairwise comparison test was performed to identify specific differences in walleye back-calculated fork length at ages 1, 2 and 3 among year classes (2000, 2001, 2002 and 2003).

Results

Body-Scale Relationship

Scale samples from age 0 to age 5 walleye of all sampling locations (western, west-central and east-central sub-basins) were used to construct body-scale relationships. The area specific body-scale relationships for walleyes were estimated (Figure 2.2) as follows:

$$\text{Western Basin: } y = -0.402x^2 + 5.856x - 14.60 \quad R^2 = 0.954$$

$$\text{West-Central Basin: } y = -0.334x^2 + 5.067x - 12.34 \quad R^2 = 0.950$$

$$\text{East-Central Basin: } y = -0.486x^2 + 6.915x - 17.97 \quad R^2 = 0.890$$

where x is the natural logarithm of fork length (FL) and y represents the natural logarithm of total scale radius (SR).

However, overlap of the 95% confidence intervals of the area specific body-scale relationships indicated that a single standard body-scale relationship for all samples collected from Lake Erie would be acceptable. By pooling all samples, the body-scale relationship used to back-calculate fork length for all samples in this study was estimated, as follows (Figure 2.3):

$$y = -0.370x^2 + 5.491x - 13.57 \quad R^2 = 0.948$$

where x equals the natural logarithm of fork length (FL) and y equals the natural logarithm of total scale radius (SR).

Walleye back-calculated fork length differences among sub-basins and year classes

Multivariate analysis of variance (MANOVA) showed that fork length-at-age of Lake Erie walleye varied significantly by sub-basin and year-class (Table 2.3). The MANOVA also indicated that the difference of length distribution among the areas depended on the year class as well (Table 2.3).

Differences in walleye fork length among the three areas

Western basin walleye mean fork length at age 1 was not significantly different from walleye mean fork length at age 1 of walleye from the west-central and east-central sub-basins combined ($F = 0.214$; $p > 0.05$; Figure 2.4). Mean fork length at age 1 of walleyes from the west-central sub-basin was not significantly different than that for the east-central sub-basin ($F = 0.464$; $p > 0.05$; Figure 2.5). The mean fork length at age 2 for western basin walleye was significantly smaller than that for west-central and east-central sub-basins walleye ($F = 8.393$; $p < 0.01$; Figure 2.6). Mean fork length of age 2 walleye in the west-central sub-basin compared to that from the east-central sub-basin was not

statistically significantly different ($F= 0.863$; $p>0.05$; Figure 2.7). The mean fork length at age 3 of western sub-basin walleye was statistically significantly smaller than that of the west-central and east-central sub-basins ($F= 23.552$; $p <0.001$; Figure 2.8). Mean fork length at age 3 of west-central sub-basin walleye was statistically significantly smaller than mean fork length of east-central sub-basin walleye at the same age ($F= 4.670$; $p<0.05$; Figure 2.9).

To summarize, walleye mean fork length at age 1 did not differ among areas of capture. However, walleye fork length at age 2 and 3 was smaller in the western basin than in the west-central and east-central sub-basins. Furthermore, age 2 and 3 walleye caught in the west-central sub-basin were smaller than those captured in the east-central sub-basin.

Differences in walleye back-calculated fork length among year-class

Tukey post-hoc pairwise comparisons were performed to examine specific differences in walleye mean back-calculated fork length at three ages (1, 2, and 3) among four year-classes (2000, 2001, 2002 and 2003).

Age 1 walleye from the 2000 year-class were significantly larger than walleye of the 2002 and 2003 year-classes (Table 2.4). Age 1 walleye from the 2001 year-class were significantly larger than those from the 2002 and 2003 year-classes (Table 2.4). The first year growth rate of walleyes appeared to be similar for the 2000 and 2001 cohorts and for the 2002 and 2003 cohorts (Table 2.4). Age 2 walleye from both the 2000 and 2001 year-classes had significantly larger fork lengths than age 2 walleye of the 2002 and 2003 year-classes (Table 2.4). The mean fork lengths at age 2 for walleye of the 2000 and 2001 year classes were similar as were the lengths for the 2002 and 2003

cohorts (Table 2.4). Age 3 walleye from the 2002 year-class were significantly smaller than walleye of the same age from the 2000, 2001, and 2003 year-classes (Table 2.4).

In general, the growth pattern of walleye prior to age 3 was similar for the cohorts of 2000 and 2001 and for the cohorts of 2002 and 2003, with the exception that smaller age 3 walleye were observed in 2002 than 2003. Walleye of the year-classes of 2000 and 2001 were usually larger than those of the 2002 and 2003 year-classes.

Discussion

Body-Scale Relationship

The established body-scale relationship for the western basin Lake Erie walleye stock has a gap in fork lengths from approximately 200 mm to 260 mm (Figure 2.4). Most walleye with fork lengths below this size gap are age 0 fish sampled from the western and west-central sub-basins. The mean (\pm SE) fork length at capture of all age 0 walleye in the study was 173.0 ± 1.81 mm (n= 96), while the average back-calculated fork length of all age 1 walleye at their first birthday (i.e., spring) was 191.5 ± 0.78 mm (n= 816). The average fork length at capture of all age 1 walleye was 322.4 ± 0.21 mm (n= 217). These walleye were sampled in the western sub-basin during September and the west-central sub-basin during September and October; therefore, at the time of capture these walleye were at least half a year old for fish considered to be age 0 in this study and 1.5 years old for the fish considered to be age 1. It appears that little growth occurs in walleye between September/October of the year they were hatched and their first birthday (<20 mm increase in fork length during that time frame). This indicates that a significant amount of seasonal growth of age 1 walleye occurs between April and September/October (at the time of sampling), at which time walleye mean fork length is 322.4 mm. Therefore, the samples used in this study probably missed the period of rapid

growth in age 1 walleye. This would explain why fish with fork lengths of 200 to 260 mm are rarely seen in the dataset. Therefore, the size gap observed in the body-scale relationship may reflect the time of year at which sampling occurs. Zhao (2005) observed a similar gap in the body-scale relationships of western basin walleye samples and eastern basin (from the southern side of the eastern basin in Van Buren Bay of New York waters) walleye samples.

Differences in back-calculated fork length of walleye among sub-basins

Many factors influence walleye growth, including resource quality and abundance, population density, water temperatures, and migration patterns (Colby et al. 1979 in Hartman 2009; Kershner et al. 1999). In the present study, significant basin differences of walleye length were observed for age 2 (between western basin and pooled central basin) and age 3 fish: the walleye with the smallest fork lengths at ages 2 and 3 were observed in the western basin and the largest fish were captured in the east-central basin. The differences observed in walleye fork length of age 2 and age 3 fish from west to east within Lake Erie may reflect size-dependent movement among basins, whereby the larger individual walleye travel greater distances to the east. The modeling and bioenergetics studies of Kershner et al. (1999) compared Lake Erie walleye growth among western basin residents, central basin residents and walleye that migrated seasonally. Their results indicated that western basin walleye that moved from the western basin to the central basin had higher growth rates than the non-migrating walleye from the western or central basins. They argued that the cooler central basin fosters more rapid growth than the warm, shallow western basin during the summer (Kershner et al. 1999). The summer water temperature of the central basin exceeds 24° C less often than in the western basin (Kershner et al. 1999), which is above the water temperature

(20-23° C) optimal for growth of large walleye (Coutant 1977). By moving among basins within Lake Erie, walleye can take advantage of the more suitable habitat found in the other basins (central and eastern) that allow for maximal growth during the growing season.

A recent tagging study (Wang et al. 2007) supports the hypothesis of Kershner et al. (1999). Walleyes tagged in the western basin but recaptured outside of the western basin were typically larger (and also older) than fish recaptured within the western basin (Wang et al. 2007). Larger and consequently older (mostly age 2 and older) western basin walleye were found to travel eastward beginning in late spring (Wang et al. 2007). Earlier tagging studies also identified this dispersal phenomenon in adult walleye (Ferguson and Derksen 1971). The movement was proposed to be a consequence of increasing water temperatures (above what is optimal for walleye growth in the western basin) and the availability of soft-rayed prey fishes in the eastern basin of Lake Erie (Wang et al. 2007). The combination of more suitable growing conditions due to lower temperatures in the central and eastern basins and a great abundance forage fishes there may explain why the walleye captured in the west-central and east-central sub-basins are larger than those of equivalent age captured in the western basin. The smaller western basin walleye may be living in less suitable growing conditions, including higher summer water temperatures and lower prey abundances, leading to less overall growth.

In the present study, walleye fork length back-calculated at age 1 was not significantly different among the western, west-central and east-central sub-basins. Previous studies showed that young walleye remained in the western basin and rarely moved beyond it (Wolfert 1963; Ferguson and Derksen 1971). The western basin

spawning stock contributes the majority of lake-wide walleye abundance and harvest (Zhao et al. 2011). Thus, most of the walleye examined in this study likely originated in the western basin, where the shallow warm basin provides suitable spawning and nursery habitat on the southern shore (Regier et al. 1979). In the summer, however, water temperatures can increase and become sub-optimal (above 24° C) for growth of larger walleye. Western basin walleye have been suggested to spend up to their first two years in the western or west-central basins and start their eastward travel only after age 2 (Wang et al. 2007). Therefore, walleye growth and back-calculated fork length at age 1 would be similar regardless of their sub-basin of capture because they likely experienced the same environmental conditions before age 2.

The varying environmental conditions among Lake Erie's basins likely provide different habitats for walleye at different stages during their life and are a probable explanation for the differences observed in size-at-age. The smaller, younger walleye are confined to the warmer western basin where there is abundant suitable spawning and nursery habitat. But once walleye reach the age of 2 or older they are able to migrate to other basins within Lake Erie and select habitat that optimizes their growth at age.

Differences in back-calculated fork length of walleye among year classes

Since walleye growth can be influenced by both abiotic and biological factors (Craig 2000), it is expected that walleye fork length back-calculated at ages 1, 2, and 3 could be different among year classes. Overall, the fish from the 2000 and 2001 year-classes were larger than those from the 2002 and 2003 year-classes. This was especially true of the 2003 year-class, which is the strongest year-class observed during the past 30 years (WTG 2010). The observed smaller walleye sizes at ages for the 2003 year-class possibly reflect density dependent effects - slower growth rates because of fewer

available resources for each fish. Another explanation is that the strong 2003 year-class walleyes increased total walleye abundance when they partially recruited to the fisheries at age 2 and 3. This led the Lake Erie fisheries management agencies, which use an abundance-based harvest policy, to set a high harvest quota for walleye fisheries in subsequent years. Consequently, the 2003 year-class fish likely experienced a higher fishing mortality rate at the recruitment ages than the other year-classes. The high fishing pressure may effectively remove the larger age 1, 2, and 3 walleye and leave disproportionately more smaller fish in the population, possibly explaining the observed smaller lengths-at-age. A study of the effects of size-selective fishing pressures on walleye growth is presented in the next chapter.

Overall, walleye growth was found to vary among sampling areas and year-classes; these results corroborate the findings of previous studies (Wolfert 1963; Kershner et al. 1999; Wang et al. 2007). These differences are likely the result of size-dependent dispersal of walleye, differing environmental conditions among Lake Erie's basins, density-dependent effects and/or abundance-based harvests. This study provides a snapshot in time of walleye size-at-age from the western and central basins. This information should be used to monitor the western basin walleye population's length changes over time for proper management of the species.

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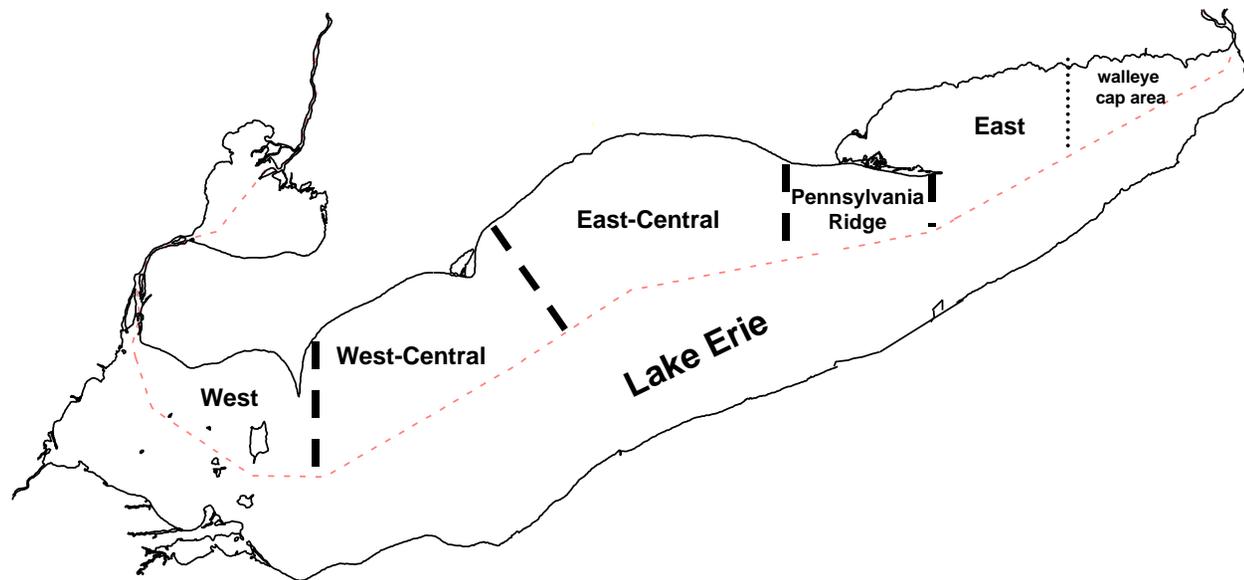


Figure 2.1 Map of Lake Erie showing the location of sampling areas, the Canadian waters of the West, West-Central, and East-Central basins (From 2006 Lake Erie Partnership Index Fishing, Project Description and Sampling Protocol).

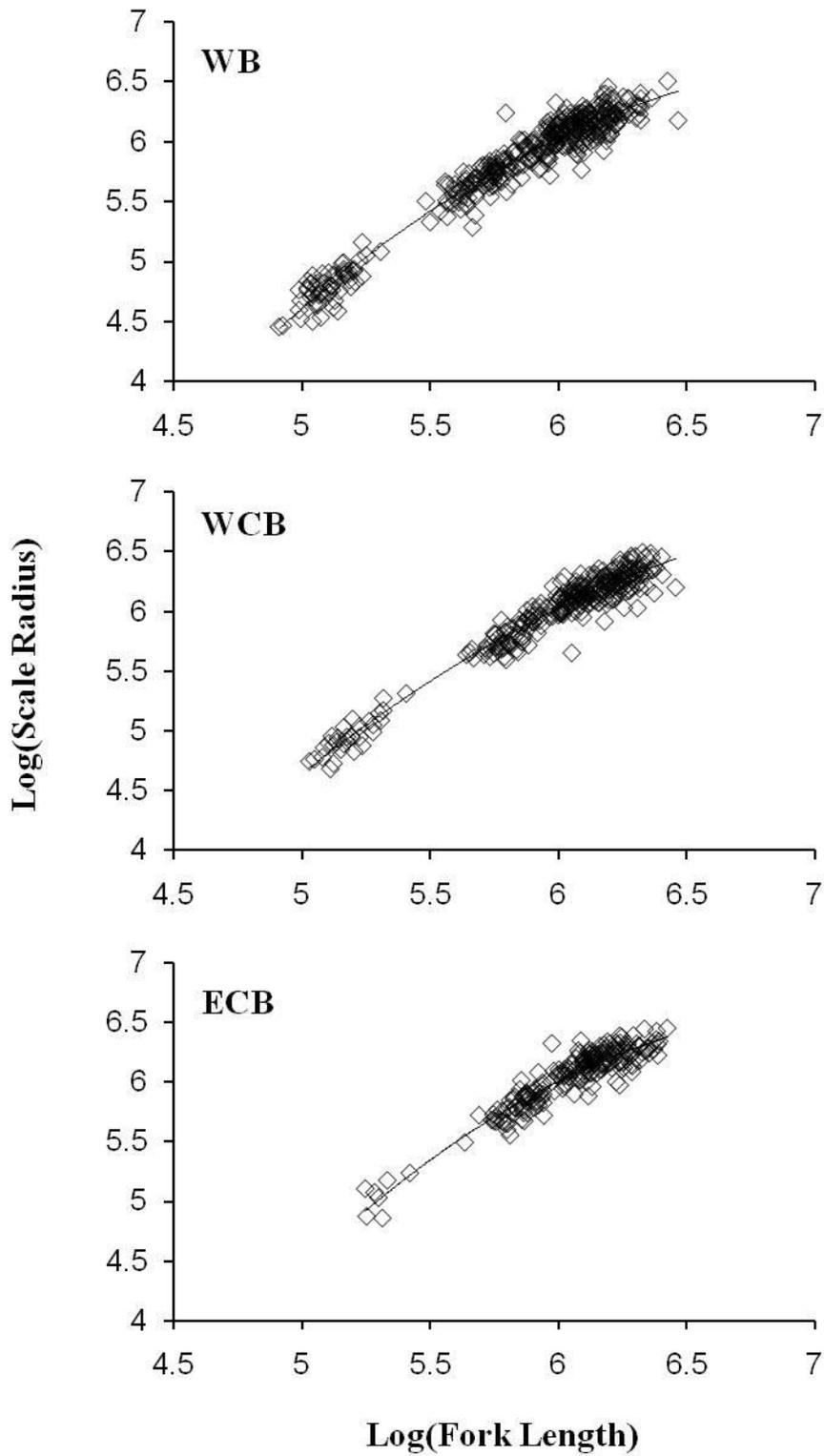


Figure 2.2 Body length-scale relationships for each sampling area in Lake Erie: west basin (WB), west-central basin (WCB) and east-central basin (ECB).

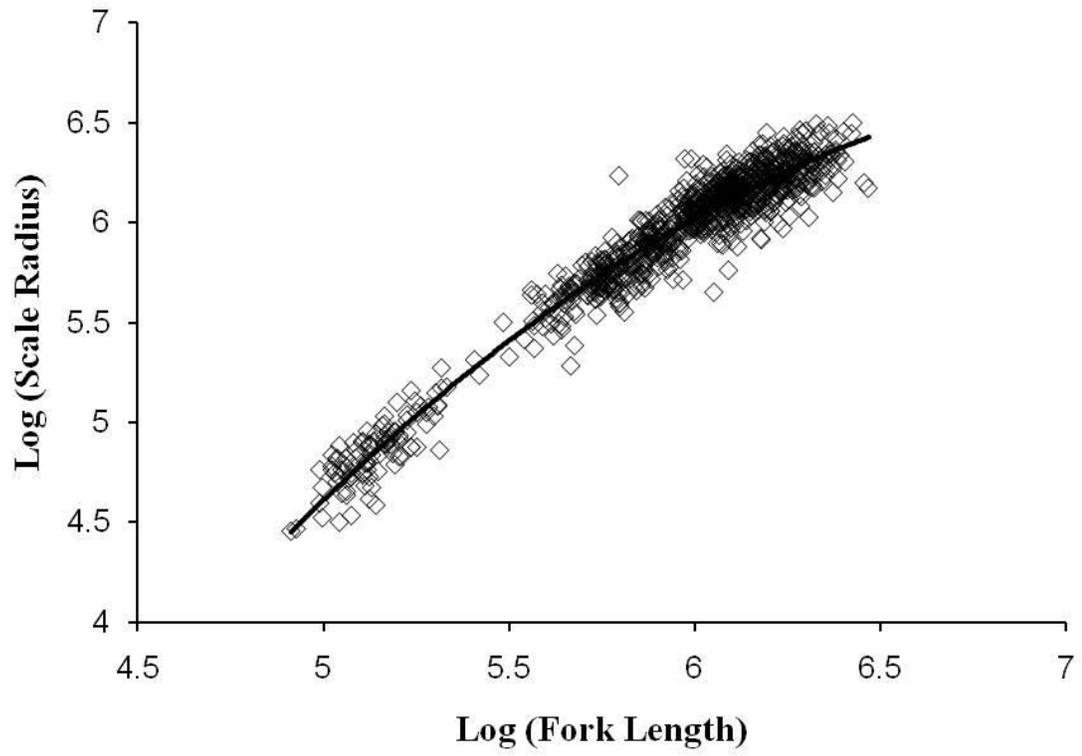


Figure 2.3 Pooled body length-scale relationship for all western basin walleye population samples.

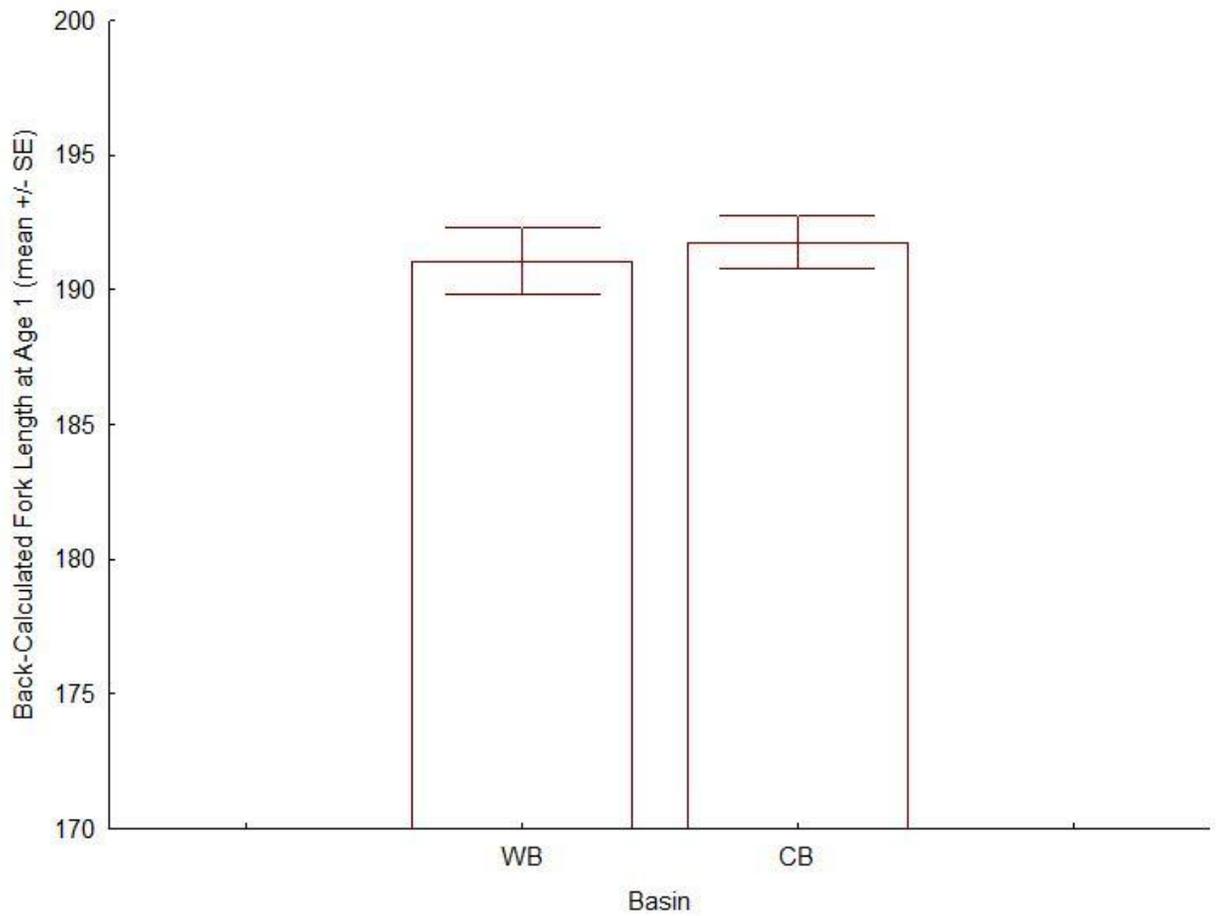


Figure 2.4 Mean (\pm S.E.) back-calculated fork length (mm) of age 1 walleye collected from western (WB) and central (CB) basins. Mean back-calculated fork length at age 1 was not significantly different between the western and central basins.

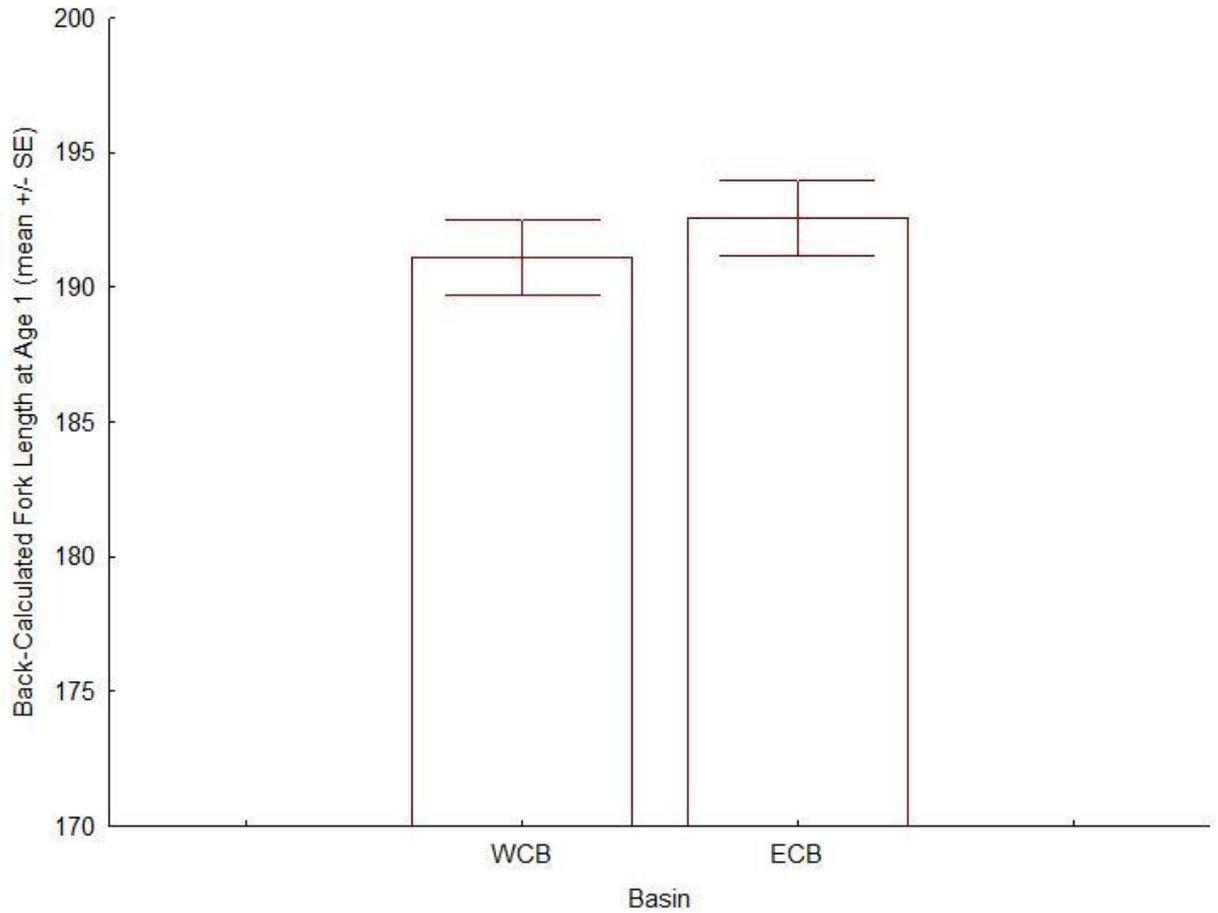


Figure 2.5 Mean (\pm S.E.) back-calculated fork length (mm) of age 1 walleye collected from west-central (WCB) and east-central (ECB) sub-basins. Mean back-calculated fork length at age 1 was not significantly different between the west-central and east-central sub-basins.

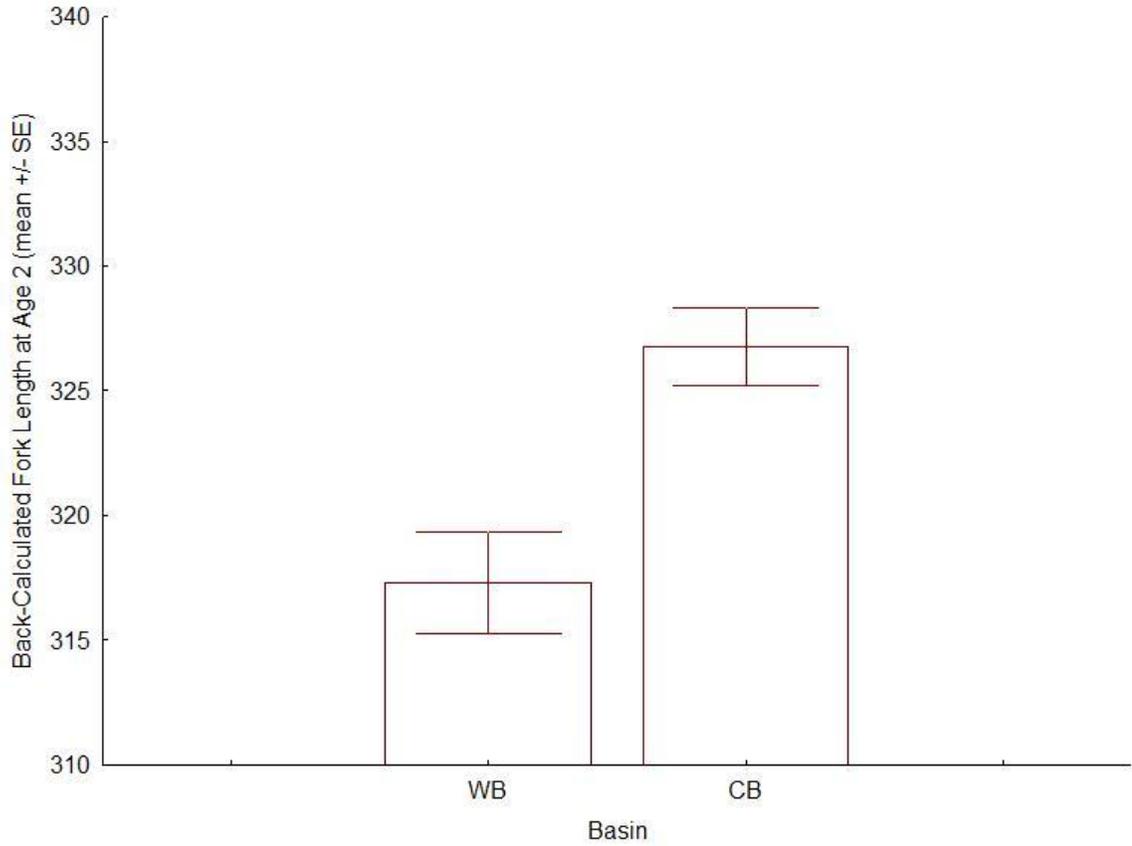


Figure 2.6 Mean (\pm S.E.) back-calculated fork length (mm) of age 2 walleye collected from western (WB) and central (CB) basins. Mean back-calculated fork length at age 2 was significantly smaller for western basin walleye than central basin walleye.

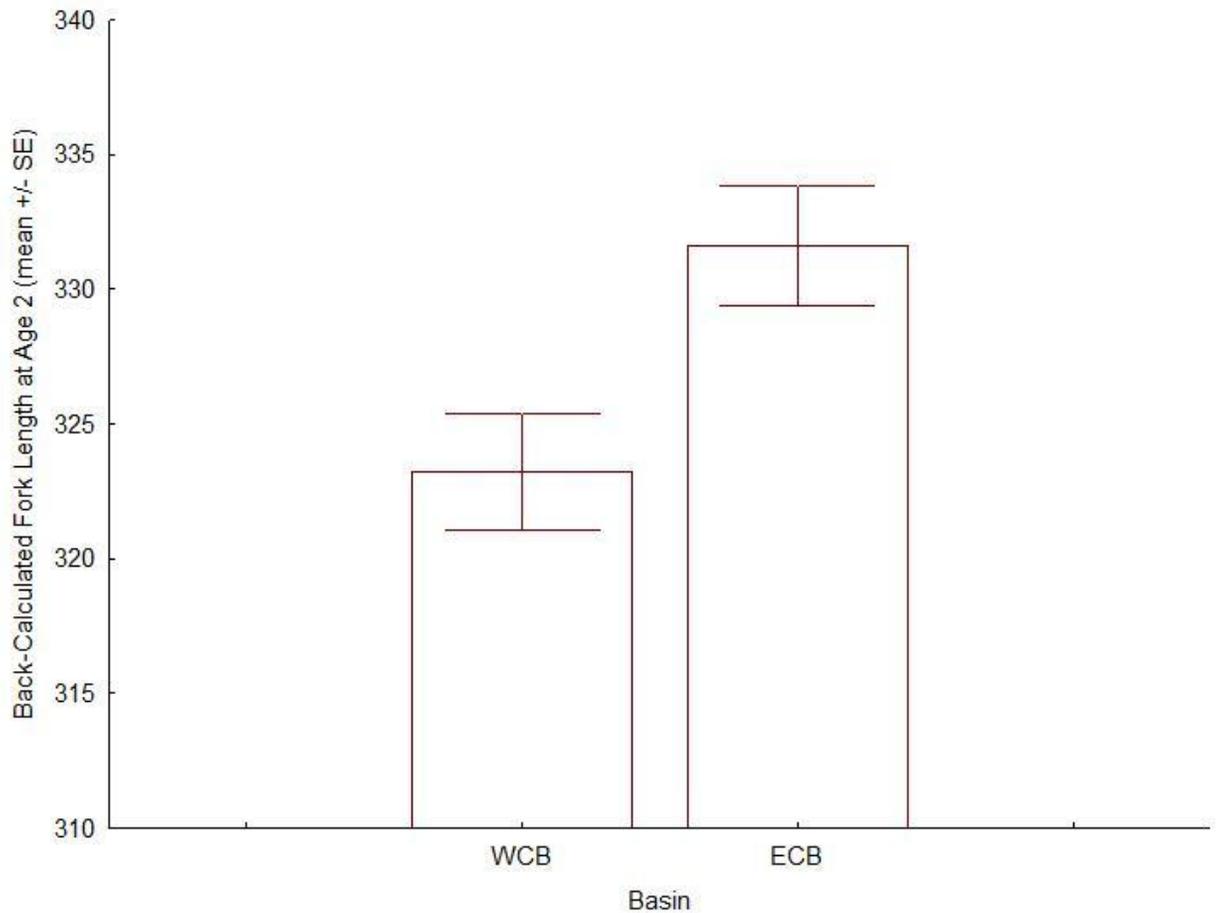


Figure 2.7 Mean (\pm S.E.) back-calculated fork length (mm) of age 2 walleye collected from west-central (WCB) and east-central (ECB) sub-basins. Mean back-calculated fork length at age 2 was not significantly different between the west-central and east-central basins.

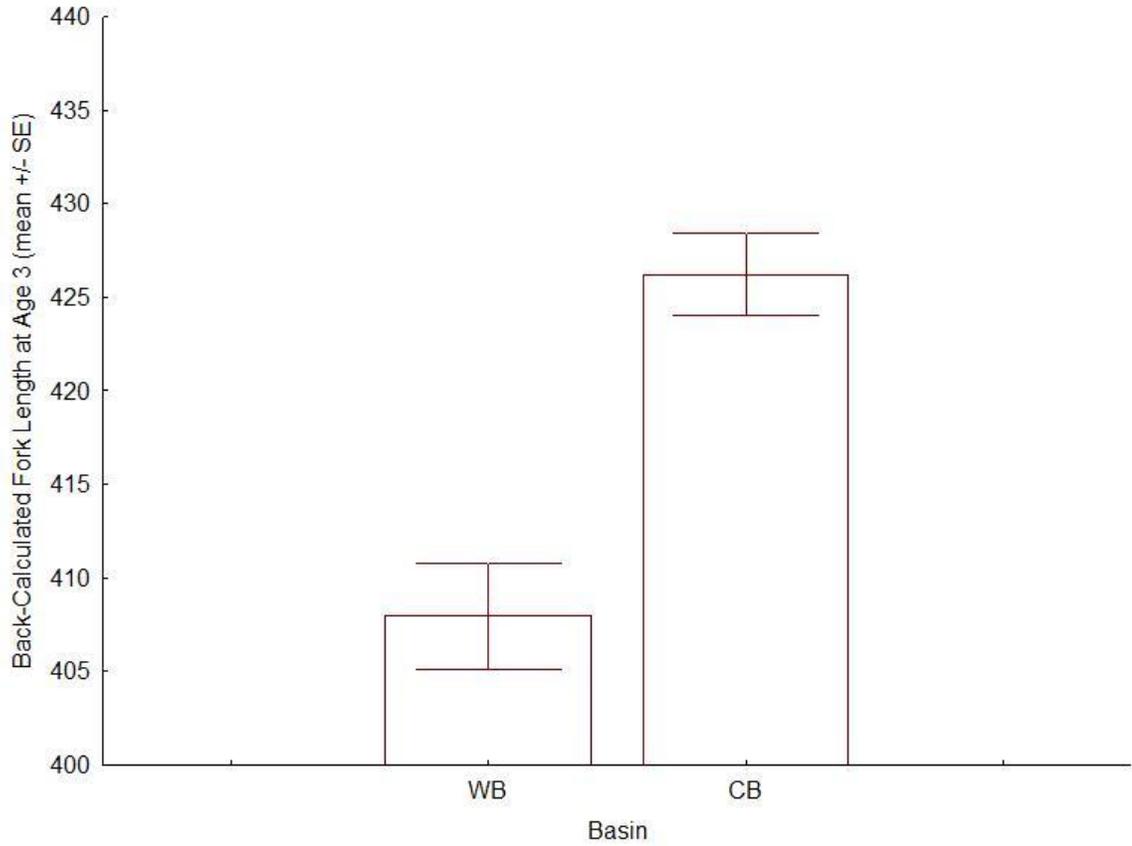


Figure 2.8 Mean (\pm S.E.) back-calculated fork length (mm) of age 3 walleye collected from western (WB) and central (CB) basins. Mean back-calculated fork length at age 3 was significantly smaller for western basin walleye than central basin walleye.

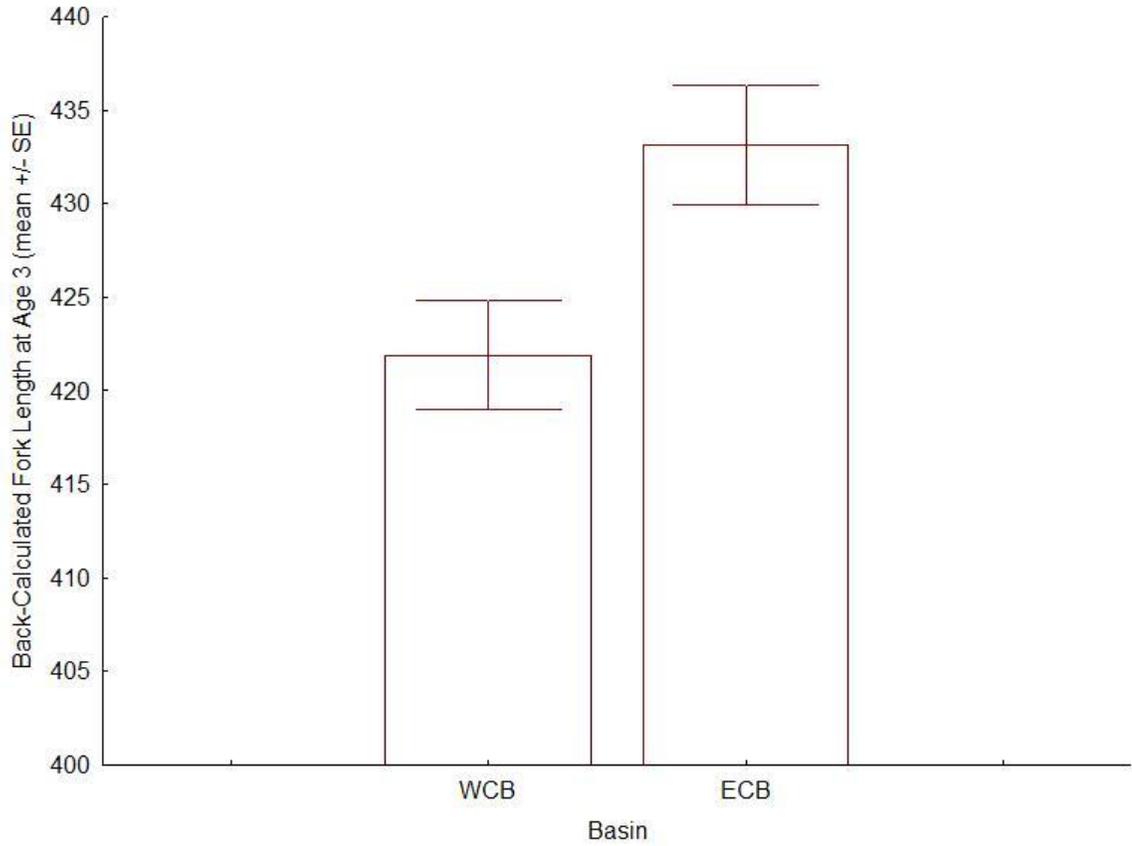


Figure 2.9 Mean (\pm S.E.) back-calculated fork length (mm) of age 3 walleye collected from west-central (WCB) and east-central (ECB) sub-basins. Mean back-calculated fork length at age 3 was significantly smaller for west-central basin walleye than east-central sub-basin walleye.

Table 2.1 Summary of the surface areas (km²), mean depths (m), maximum depths (m), mean water temperatures (°C) (1967-1982), and mean near-bottom temperatures (°C) for each basin (western, central, and eastern) and the entire lake (Schertzer et al. 1987; Bolsenga and Herdendorf 1993).

Parameter	Western Basin	Central Basin	Eastern Basin	Entire Lake
Surface area (km ²)	3,284	16,138	6,235	25,657
Mean depth (m)	7.4	18.5	24.4	18.9
Maximum depth (m)	18.9	25.6	64.0	64.0
Mean water temperature °C (1967-1982)	17.27	14.85	14.71	-----
Mean near-bottom temperature °C in August (estimated from Schertzer et al. 1987)	22	13	6	-----

Table 2.2 Number of walleye samples collected from each sampling area: western basin (WB), west-central basin (WCB), and east-central basin (ECB).

Year-Class	Age at Capture	Sample Size		
		WB	WCB	ECB
2000	0	0	0	0
	1	30	0	0
	2	24	4	3
	3	16	5	3
	4	7	8	4
	5	2	1	0
2001	0	29	1	0
	1	30	29	30
	2	31	29	30
	3	30	30	30
	4	30	30	7
	5	16	11	5
2002	0	0	0	0
	1	8	1	0
	2	1	1	0
	3	8	3	0
	4	1	2	1
	5	0	3	2
2003	0	29	30	7
	1	31	29	29
	2	30	30	30
	3	28	25	24
	4	18	24	12
	5	0	0	0

Table 2.3 Results of the multivariate analysis of variance testing for differences in walleye mean back-calculated fork length at ages 1, 2 and 3 among sampling areas and year-classes. The univariate results are presented for each age below the MANOVA results.

Effect	Wilks Value	F	Effect d.f.	Error d.f.	P
Basin	0.888	7.578	6	744	<0.001
Year-Class	0.587	24.653	9	905	<0.001
Basin*Year-Class	0.851	3.423	18	1052	<0.001

Age 1					
Factor	df	SS	MS	F	p
Basin	2	188	94	0.27	>0.05
Year-Class	3	56385	18795	54.41	<0.001
Basin*Year-Class	6	3513	585	1.69	>0.05
Error	374	129192	345		
Total	385	194659			

Age 2					
Factor	df	SS	MS	F	p
Basin	2	6412	3206	4.20	<0.05
Year-Class	3	66941	22314	29.25	<0.001
Basin*Year-Class	6	11333	1889	0.02	<0.05
Error	374	285287	763		
Total	385	392190			

Age 3					
Factor	df	SS	MS	F	p
Basin	2	24592	12296	12.13	<0.001
Year-Class	3	15626	5209	5.14	<0.01
Basin*Year-Class	6	23612	3935	3.88	<0.001
Error	374	379052	1014		
Total	385	480356			

Table 2.4 Mean fork length of walleye of ages 1, 2 and 3 in years 2000 – 2004 from all basins. Means within rows having different superscripts are significantly different from one another (Tukey post-hoc pairwise comparison, $p < 0.05$).

Age	YEAR-CLASS			
	<u>2000</u>	<u>2001</u>	<u>2002</u>	<u>2003</u>
1	196.3 ^a	197.6 ^a	178.5 ^b	170.9 ^b
2	332.5 ^a	331.1 ^a	298.2 ^b	302.8 ^b
3	428.0 ^a	422.6 ^{ac}	379.6 ^b	416.1 ^{ac}

CHAPTER 3: ESTIMATION OF SIZE-SELECTIVE MORTALITY OF WESTERN BASIN LAKE ERIE WALLEYE USING GROWTH INFORMATION

Introduction

Size-selective mortality occurs when mortality rates differ among fish of the same year-class because of differences in their body size (Ricker 1969). The degree of size-selective mortality observed within a particular year-class of fish is determined by the size distribution of that year-class. For example, if no individual size variation existed in an exploited fish population, there would be no size-selective mortality (due to exploitation) because all fish would have an equal chance of capture. However, size variation does exist within age classes of all fish populations. Therefore, all exploited fish populations are potentially susceptible to size-selective mortality because faster growing fish are likely harvested more intensely than slower growing fish since they reach a catchable size sooner than slower-growing individuals (Ricker 1981).

Recruitment in fishery science is variously defined as the number of individuals in a year class that live to reach a reproductive size, harvestable size, specific age or size, or when they become vulnerable to certain sampling gear (Willis and Murphy 1996). In this study, recruitment refers to the process whereby fish of a year-class become vulnerable to fishing gears due achieving a particular body size (Ricker 1969). Fishing gears are inherently size-selective (Sinclair et al. 2002). For example, gillnets are designed to capture the larger fish while allowing the smaller fish to pass through the net without being caught. Since fish do not become vulnerable to fishing gears at a specific age, but instead become vulnerable over a range of sizes and since size-at-age varies greatly among individuals, fishing during the recruitment phase can result in size-selective

mortality within a given age-group (Ricker 1969; Sinclair et al. 2002). In a fish population, size-selective mortality can occur from natural mortality or it can be a result of fishing mortality, where fish of different size-classes have different catchabilities (Ricker 1969). In the case of fishing, the large and fast growing fish will be removed more quickly than the smaller, slower growing fish because they become vulnerable to fishing gear earlier (Ricker 1969). Moreover, fisheries greatly influence stock abundance. Therefore, fisheries can influence a population's mean length-at-age through size-selective mortality (Sinclair et al. 2002). By heavily harvesting the larger and faster growing fish, smaller and slower growing fish remain, thus making up a larger portion of the overall fish stock, as was observed in 5 species of Pacific salmon (Ricker 1981).

Generally, larger and faster growing fish are believed to have a survival advantage over smaller, slower growing fish during early life stages because they are more competitive for resources and can develop stronger tolerances of environmental extremes (Sogard 1997). Additionally, as fish grow, mortality decreases because the number of their predators gradually changes and eventually decreases once the fish has reached a certain size (Anderson 1988). If fishing activities select larger and faster growing fish within a year-class, the mean back-calculated length at the age under consideration for the year-class will decrease in successive years (Sinclair et al. 2002). The mean back-calculated length of a year-class at an earlier age represents the length of individuals that survived to the age when they were sampled; therefore this mean back-calculated length may be different from the mean lengths of the fish directly measured at the age (Ricker 1969). This difference, considered in the context of the growth history,

can be used to quantify the size-selective mortality rates experienced by the year-class (Ricker 1969).

Ricker (1969) and Jones (1958) demonstrated size-selective mortality using a hypothetical fish population that did not grow. In their example, a year-class of fish had a normal length-frequency distribution and the instantaneous mortality rate increased by 0.1 for each 5 mm of increase in length starting with a mortality rate of zero for fish 60-65 mm in length. The cohort was simulated for several years. For each year, the mean length of survivors was calculated. Both the simulation (Ricker 1969) and the analytical study (Jones 1958) showed that the mean size of the year-class decreases, but the general shape of the distribution and variation are conserved.

Previous studies have found changes in life history traits due to size-selective fishing in multiple species (Ricker 1981; Chen and Mello 1999; Conover and Munch 2002; Fenberg and Roy 2008). Five species of Pacific salmon were found to have decreased in body size over time. This was speculated to be due to size-selective fishing of larger fish (Ricker 1981). Size-at-age of cod from the Northwest Atlantic was found to decrease over a period of about two decades (1970s to 1990) resulting from intense selective fishing of larger (assumed to be faster growing) fish (Chen and Mello 1999). Year-classes of cod with smaller size-at-age were generally found to mature faster (Chen and Mello 1999). Conover and Munch (2002) used a laboratory experiment to demonstrate that size-selective mortality of Atlantic silversides (*Menidia menidia*) targeting either large or small fish resulted in differences in production. Lower yields were produced by the populations where large silversides were harvested and higher yields were produced by the populations where small silversides were harvested,

compared to populations that were randomly harvested (Conover and Munch 2002). The changes in yields were attributed to selection for faster growth rates (in populations where smaller fish were size-selectively harvested) or slower growth rates (in populations where larger fish were size-selectively harvested) (Conover and Munch 2002).

In this study, I used the scales collected from a fishery-independent survey program to back-calculate the fork lengths of walleyes from three year-classes, 2000, 2001 and 2003, in the western basin of Lake Erie. The 2002 year-class was excluded from this study because of small sample sizes, especially of older-age fish. For each year-class, the calculated growth information was used to estimate (1) the age at which size-selective mortality rate may have started, (2) the size-selectivity mortality rate, and (3) differences in the selectivity intensity between large and small fish. I expected to find size-selective mortality of walleye within a year-class to occur at either age 1, 2 or 3 due to the variability in individual size among fish and size at recruitment to Lake Erie's commercial and sport fisheries. After age 3, walleye are thought to be fully recruited to the fishery (WTG 2010); therefore I did not expect to find size-selective mortality in fish older than age 3 because all such walleye would be equally vulnerable to fishing gears.

Materials and Methods

Study Area

The walleye samples used in this study were collected from the Canadian waters of Lake Erie through a partnership survey program (Great Lakes Fishery Commission, Lake Erie Committee Partnership Index Gillnetting Program unpubl; Ontario Ministry of Natural Resources Lake Erie Management Unit and the Ontario Commercial Fisheries Association 2006). Lake Erie, which is the shallowest and warmest Great Lakes

(Schertzer 1999; Rasul et al. 1999), has three distinct basins: western, central and eastern, which have temperature and limnological differences.

To reduce the influence of the eastern basin walleye stock, only samples collected from the western and central basins were used for this study. The central basin was further divided into the west-central sub-basin and the east-central sub-basin, which resulted in three sampling areas for this study: the western basin, west-central sub-basin and east-central sub-basin. Fish were sampled annually within these 3 areas for at least nine consecutive years. Scales collected from fish captured between 2000 and 2008 were used in this study, representing cohorts that were spawned in four calendar years: 2000-2003. Chapter 2 provides a more detailed description of the study area.

Age estimation and measurement of walleye scales

The Ontario Ministry of Natural Resources staff performed preliminary aging of all walleye scale samples. After the initial aging, up to 30 fish from each age-group (age 0 to 5) for each year-class (2000, 2001, and 2003) of each area (western basin, west-central sub-basin, and east-central sub-basin) were randomly selected for use in this study. I examined the scale impressions under a microfiche projector at 40X magnification, and thus aged them a second time. Ages were estimated by enumerating the annuli on each scale along the anterior-posterior axis. If the original and my confirmatory age estimations disagreed, the sample was discarded from the study. For each sample, the scale focus (center of the scale), each annulus and the scale margin (edge of the scale) were recorded on a strip of plastic transparency approximately 2.5 cm wide using a permanent marker. These marks were digitized using a SummaSketch II professional digitizer to measure the distance from the scale focus to each annulus. These distances were used to estimate each individual walleye's previous fork lengths at

age. A more complete description of the age estimation and measurement of scales is provided in Chapter 2.

Walleye body-scale relationship

The pooled body-scale relationship equation as per Chapter 2 was used.

Back-calculation of fork length-at-age

Earlier length-at-age for each individual walleye was estimated using the back-calculation procedure provided in Chapter 2.

Estimation of size-selective mortality

Simple linear regression was used to test for a relationship between back-calculated fork length at a given age (age 1, 2, or 3) and back-calculated fork lengths at the given age at successive years of capture, ages 1 through 5, for year-classes 2000, 2001, and 2003. Samples from the three sampling areas were combined and considered to belong to the western basin Lake Erie stock. A total of 776 walleye samples were included in the size-selective study: 107 samples from the 2000 year-class, 368 from the 2001 year-class and 301 from the 2003 year-class. The statistical significance level was set at $\alpha = 0.05$. A slope different from zero indicates size-selective mortality; a negative slope indicates a decrease in mean fork length as age at capture increases, suggesting selection for smaller fish, while a positive slope shows that mean fork length increases as age at capture increases, indicating selection for larger walleye (Sinclair et al. 2002). Because I postulated that size-selective mortality should produce a negative slope, I employed a one-tailed test. Since the slope of the regression line is equal to the change in mean fork length of walleye from one year to the next, it was used to estimate instantaneous size-selective mortality, a , occurring within a year-class using the following equation:

$$a = d / s^2$$

where a is the difference in instantaneous mortality rate, during the given year, between fish that differ in size by 1 unit of length, d is the decrease in mean length of fish in one year within an age-group, and s is the standard deviation of the length distribution and estimated from the pooled back-calculated length at each age (Ricker 1969). The delta method was used to calculate the standard deviations of the size-selective mortality estimates (a). The covariance between the standard deviation of the length distribution (s) and the decrease in mean length of fish in one year within an age-group (d) was assumed to be zero.

Index of intensity of selection

The intensity of the size-selection was estimated using the selectivity index (r) described by Ricker (1969) for walleye back-calculated fork length at ages 1, 2 and 3 for all year-classes (2000, 2001, and 2003). The values were calculated using the following equation:

$$r = 1.349 * a * s$$

where r equals the difference in mean instantaneous mortality rate between fish in the smaller and larger halves of an age-group (Ricker 1969). The selection index value measures how selection is greater for the larger fish than the smaller fish of an age-group. The standard deviations of the selection index (r) were obtained using the delta method. The covariance between the standard deviation of the length distribution (s) and the decrease in mean length of fish in one year within an age-group (d) was assumed to be zero.

Results

Changes in mean back-calculated fork lengths in successive years of capture

Two strong cohorts, 2001 and 2003, and one weaker cohort, 2000, are included in this study (WTG 2010). There were 107, 368, and 310 walleye samples in the 2000, 2001, and 2003 year-classes, respectively. Few age 5 fish had been captured for the 2000 year-class, and the 2003 year-class had no age 5 samples.

Regression analyses revealed that mean back-calculated fork length of the western basin stock of Lake Erie walleye at ages 1, 2 or 3 each significantly decreased with an increase in the age when they were sampled for all year-classes (2000, 2001, and 2003) with the exception of the age 3 walleye from the 2000 year-class (Figures 3.1-3.3; Table 3.1). Overall, the back-calculated fork lengths-at-age from older fish were smaller than those from younger fish, indicating selection for fish with smaller size-at-age. The mean back-calculated fork length at ages 1, 2 and 3 decreased by no more than 10 mm per year for all cohorts except for the 2003 year-class back-calculated fork length at age 3, which was greater than a 10 mm decrease per year (Table 3.2).

Estimation of size-selective mortality

For this study, size-selective mortality was considered to be the difference in instantaneous mortality rate during a given year, between fish of the same year-class that differ in size by 1 mm of length (Ricker 1969). Size-selective mortality was estimated for the age-groups (i.e., 1, 2, and 3) of all year-classes (2000, 2001 and 2003) that showed a significant decrease in mean fork length at age as age at capture increased. Thus, size-selective mortality was estimated for age 1 and 2 walleye of all year-classes and age 3 walleye of the 2001 and 2003 year-classes.

Age 1 and age 2 walleye of all year-classes show evidence of size-selective mortality. However, only the 2001 and 2003 year-class age 3 walleye displayed evidence of size-selective mortality. For all cohorts, size-selective mortality was strongest for the fish at age 1, followed by the fish at age 2, and then by age 3 fish for the cohorts of 2000 and 2001 (Table 3.2). The 2003 cohort exhibited stronger size-selective mortality at age 3 than at age 2 (Table 3.2). These results indicated differential survival of smaller individuals; therefore, relatively smaller fish are surviving to older ages and produced a trend of decreasing mean length at a young age progressively back-calculated from fish at old ages (Figures 3.1-3.3). Size-selective mortality of western basin Lake Erie walleye never exceeded -0.027 per mm of length and was as small as -0.008 per mm of length (Table 3.2).

Index of intensity of selection

The index of intensity of selection was calculated for the age-groups of the year-classes that exhibited evidence of size-selective mortality (age 1 and 2 for all year-classes and age 3 for the 2001 and 2003 year-classes) to provide a standardized unit of selectivity not based on mean size or variability (Ricker 1969). The index of intensity of selection tells the difference in mean instantaneous mortality rate between the smaller and larger portions of an age-group (Ricker 1969). At age 1, walleye of the 2000 year-class experienced the greatest selection intensity (r), followed next by the 2003 year-class and then the 2001 year-class (Table 3.2). At age 2, the 2000 year-class walleyes experienced the highest selection intensity (r), then the 2003 year-class walleyes, and then the 2001 year-class walleyes (Table 3.2). At age 3, walleye of the 2003 year-class experienced the greatest selection intensity (r), followed by the 2001 walleyes, and then the 2000 walleyes (Table 3.2). Within the 2000 year-class, the selection intensity decreased from

age 1 to age 3, but this pattern was not seen in either the 2001 or 2003 year-classes (Table 3.2). The 2001 year-class of walleye had the greatest selection intensity at age 2, followed by age 3, and then age 1 (Table 3.2). Walleye of the 2003 year-class had the highest selection intensity at age 3, followed by age 1, and then age 2 (Table 3.2).

Discussion

Since the Lake Erie walleye population is subject to heavy fishing pressure, the population likely meets the three requirements necessary for size-selective mortality to occur within a population as described by Sogard (1997): (1) individual size variation, (2) high mortality, and (3) non-random mortality. The Walleye Task Group (2010) estimated that Lake Erie walleye are fully recruited to fishing gears by age 3. Therefore, I expected that the back-calculated size differences resulting from size-selective mortality could be detected in fish of age 1 to age 3 in this population. It was unexpected that Lake Erie walleye older than age 3 would experience size-selective mortality.

Regression analyses generally showed that the mean fork-lengths at ages 1, 2 and 3 back-calculated from scales decreased with increasing age at capture, which suggested that walleye caught at older ages (i.e., ages 4 or 5) were proportionately smaller than those caught at younger ages (i.e., ages 1, 2 or 3) for the year-classes under investigation (with the exception of age 3 walleye from the 2000 year-class). This decrease in mean fork-length indicates differential survival, and hence selection for smaller individuals (Sinclair et al. 2002). Although the average annual decreases in mean fork length of all year-classes at ages 1, 2 and 3 were small in absolute magnitude, there is still an implication that larger faster growing walleye within each age-group were more heavily harvested than the smaller individuals of the same age-group. Therefore, the smaller,

slower growing walleye tended to better survive to older ages than their larger and faster growing counterparts.

The specific cause of size-selective mortality of age 1, 2 and 3 western basin Lake Erie walleye of the 2000, 2001 and 2003 year-classes is uncertain. The most likely cause is the pressure of the recreational and commercial walleye fisheries. In 1982, the Ontario Ministry of Natural Resources required that gillnets with mesh no smaller than 89 mm stretched be used in the walleye commercial fishery; this net size targets walleye with total lengths between 406 and 533 mm, which are the most profitable size (Vandergoot et al. 2010). Additionally, in 2004, the Ohio Department of Natural Resources established a minimum size limit for the recreational walleye fishery of 381 mm. The State of Michigan also increased their minimum size limit from 330 mm to 381 mm to prevent the harvesting of age 1 walleyes (Vandergoot et al. 2010). However, this increase in the minimum size limit did not prevent the recreational harvesting of age 1 walleyes of the year-classes included in this study because it went into effect when these walleye were older than age 1. Therefore, any age-group of walleye whose total lengths fall both in and outside of the 330 to 533 mm size range, could possibly experience size-selective mortality. This fishable size range potentially explains why size-selective mortality was observed at ages 1, 2 and 3.

Further support of the possibility that the commercial and recreational walleye fisheries are causing size-selective mortality of the western basin Lake Erie walleye is evident in the large numbers of walleye aged 1, 2 and 3 harvested from the 2001 and 2003 year-classes. The Walleye Task Group reported that in 2003 age 2 walleye (of the 2001 year-class) contributed largely to the total harvests of the commercial fishery

(26.4%) and sport fishery (18.1%) (WTG 2004). During 2004, age 3 walleye of the 2001 year-class comprised 49% and 46% of the total commercial and recreational fisheries, respectively; and age 1 walleye of the 2003 year-class made up 27% of the total commercial harvest (WTG 2005). Additionally, the 2003 year-class at age 2 and age 3 largely contributed to the commercial fishery harvests; in 2005, 47% of the total commercial catch was age 2 walleye, while in 2006, 89% of the commercial harvest and 76% of the total sport fishery harvest were age 3 walleye (WTG 2006, 2007). These large contributions of age 1, 2 and 3 walleye from the 2001 and 2003 year classes to commercial and recreational fisheries are a possible explanation of the occurrences of size-selective mortality that were observed in this study. However, the cause of size-selective mortality of the 2000 year-class walleye is especially uncertain. Since the 2000 year-class was a weaker year-class it likely did not make up a large portion of the commercial or recreational harvests but most likely experienced the same selective fishing pressures.

An alternative/additional cause of size-selective mortality of age 1 walleye is the Ontario yellow perch commercial fishery. In Lake Erie, Age 1 walleye are caught as bycatch in gillnets set by the Ontario yellow perch commercial fishery (WTG 2005). However, the frequency of walleye bycatch by this fishery has not been determined.

Size-selective mortality was not expected to be found in fish older than age 3 because they are thought to be fully recruited to the fishery (WTG 2010). It is possible that not all age 3 walleye have reached recruitment size by the end of their third year of life, which would result in differential mortality based on body size. Age 3 walleye of the 2000 year-class did not exhibit a significant decrease in mean fork length as age at

sampling increased. However, lower size-selective mortality was observed compared to the other year-classes at this age. Muth and Wolfert (1986) found that at high abundances, walleye growth decreased and maturity was delayed, perhaps due to strong competition for food resources. The greater walleye abundances in the 2001 and 2003 year-classes paired with potentially low resource availability may explain why these two cohorts exhibited greater size-selective mortality at age 3 than the 2000 weaker year-class. It is also possible that the 2000 year-class experienced a lesser degree of size-selective mortality because when abundance is low, the fishing quota is reduced, possibly resulting in less fishing pressure.

The effects of size-selective mortality on the western basin Lake Erie walleye population are of concern because the selective removal of larger and faster growing individuals has can cause rapid evolution of certain traits such as growth rates and size-at-age (Law 2000; Stokes and Law 2000; Sinclair et al. 2002; Swain et al. 2007). The long term effects of size-selective mortality of this population are unknown. However, previous studies of commercially and recreationally fished populations have shown changes in growth rate, body size and/or size or age at maturation due to size-selective mortality. For example, decreases in mean sizes observed in bluegill, yellow perch, pumpkinseeds, largemouth bass, and northern pike were attributed to recreational fishing (Goedde and Coble 1981; Coble 1988). Swain et al. (2007) predicted that slower growth (and thus smaller size-at-age) of the commercially harvested southern Gulf cod population is an evolutionary result of size-selective fishing mortality where larger and faster-growing fish were more heavily harvested. Thus, this walleye population is probably currently undergoing evolution of certain traits (such as reduced growth rates,

size-at-age and age- and length-at-maturity) and may have been for quite some time since regular commercial fishing of the species has taken place for almost 200 years (Regier et al. 1969).

Future studies should focus on the long term effects (phenotypic and/or genetic) that size-selective mortality may have on this population and should be considered in future management decisions. In the future, I would expect to see a phenotypic decrease in mean size-at-age (because of slower growth rates) in response to heavy size-selective mortality of larger individuals. The time needed for size-selection to cause evolution of these traits in wild populations may vary due to variability in environmental conditions and overlapping generations (Conover and Munch 2002), but the time needed could be as short as what is necessary for a few generations to experience the selection pressure (Conover et al. 2009). Adjustments to fishing regulations could be used to accommodate current walleye growth trends and may alleviate some of the size-selective fishing pressure, since altering recreational fishing regulations and commercial net sizes can change the “window of vulnerability to the fishery” (Sinclair et al. 2002). Currently, the commercial and recreational walleye fisheries rely on minimum size limits in order to protect smaller fish, likely causing the size-selective harvesting of larger (faster-growing) fish. Conover and Munch (2002) suggest the idea of a maximum size limit to protect fish over a certain length so that larger faster growing fish spend less time vulnerable to the selective fishing gears. Thus, faster-growing fish would be favored. Consequently, I think that this form of size regulation would leave smaller, young and likely premature fish more vulnerable to selective fishing pressures for a longer period of time and cause size-selective mortality in the opposite direction of what was observed in this study. This

is likely inadvisable as well because natural genetic variation within the population may not be preserved. Therefore, future studies could implement some type of slot limit whereby intermediate size ranges are targeted to assess whether size-selection of either the faster or slower growing fish is prevented. This type of size regulation may better protect the smallest (slow growing) and largest (fast growing) portions of the population and if so, potentially conserve genetic variation.

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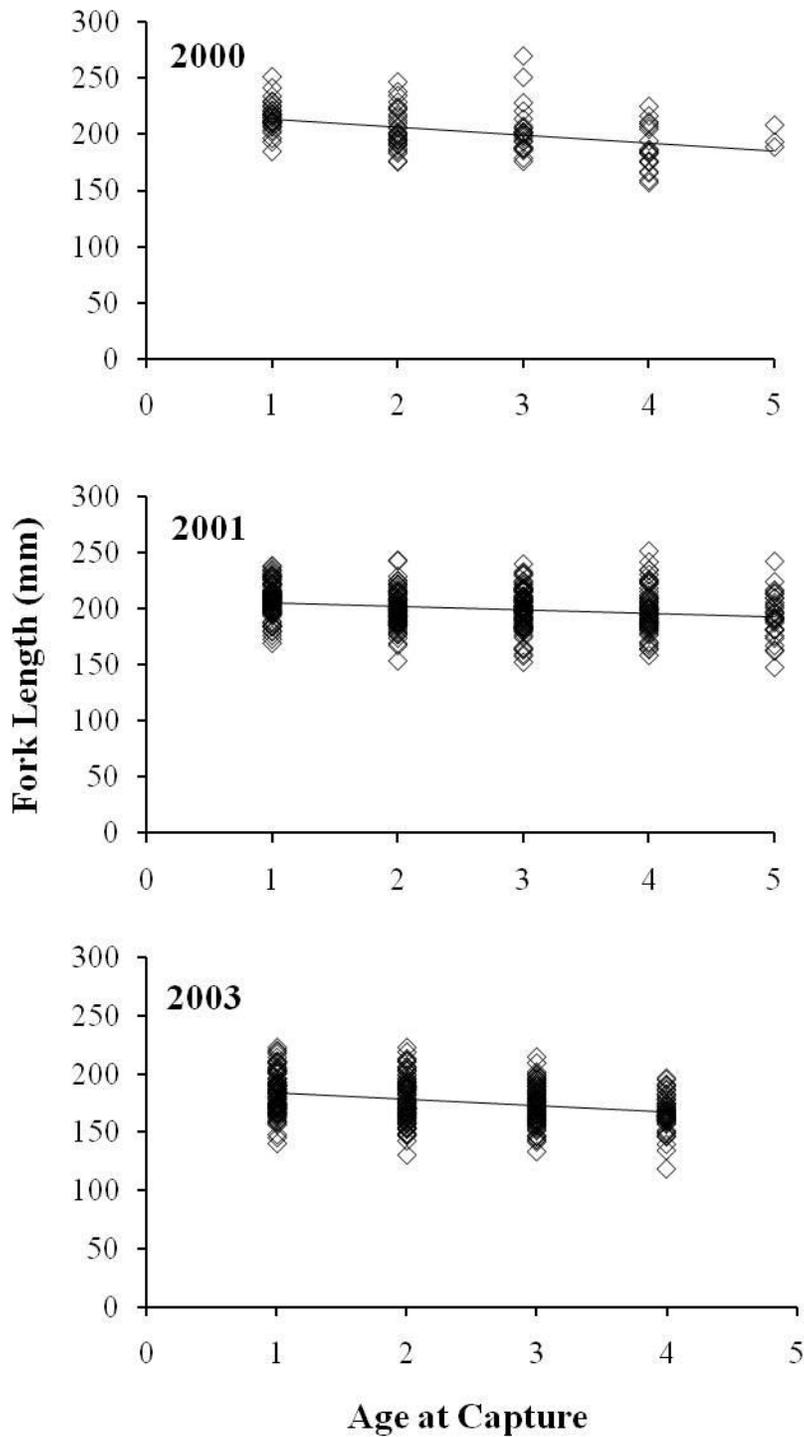


Figure 3.1 Regressions of back-calculated fork length at age 1 vs. age at capture for the 2000, 2001, and 2003 year-classes. Mean back-calculated fork length at age 1 decreased significantly as age at capture increased for all year-classes.

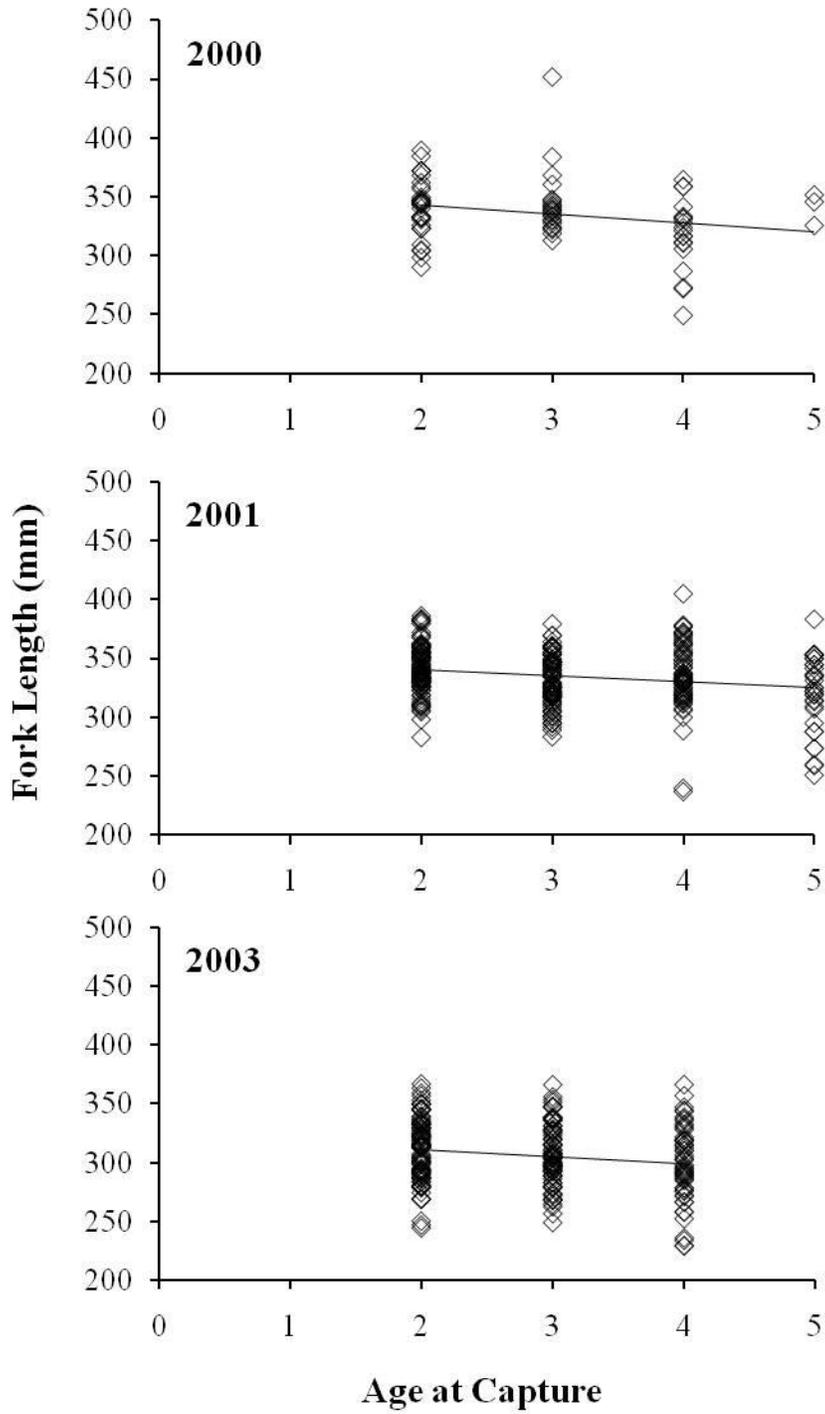


Figure 3.2 Regressions of back-calculated fork length at age 2 vs, age at capture for the 2000, 2001, and 2003 year-classes. Mean back-calculated fork length at age 2 decreased significantly as age at capture increased for all year-classes.

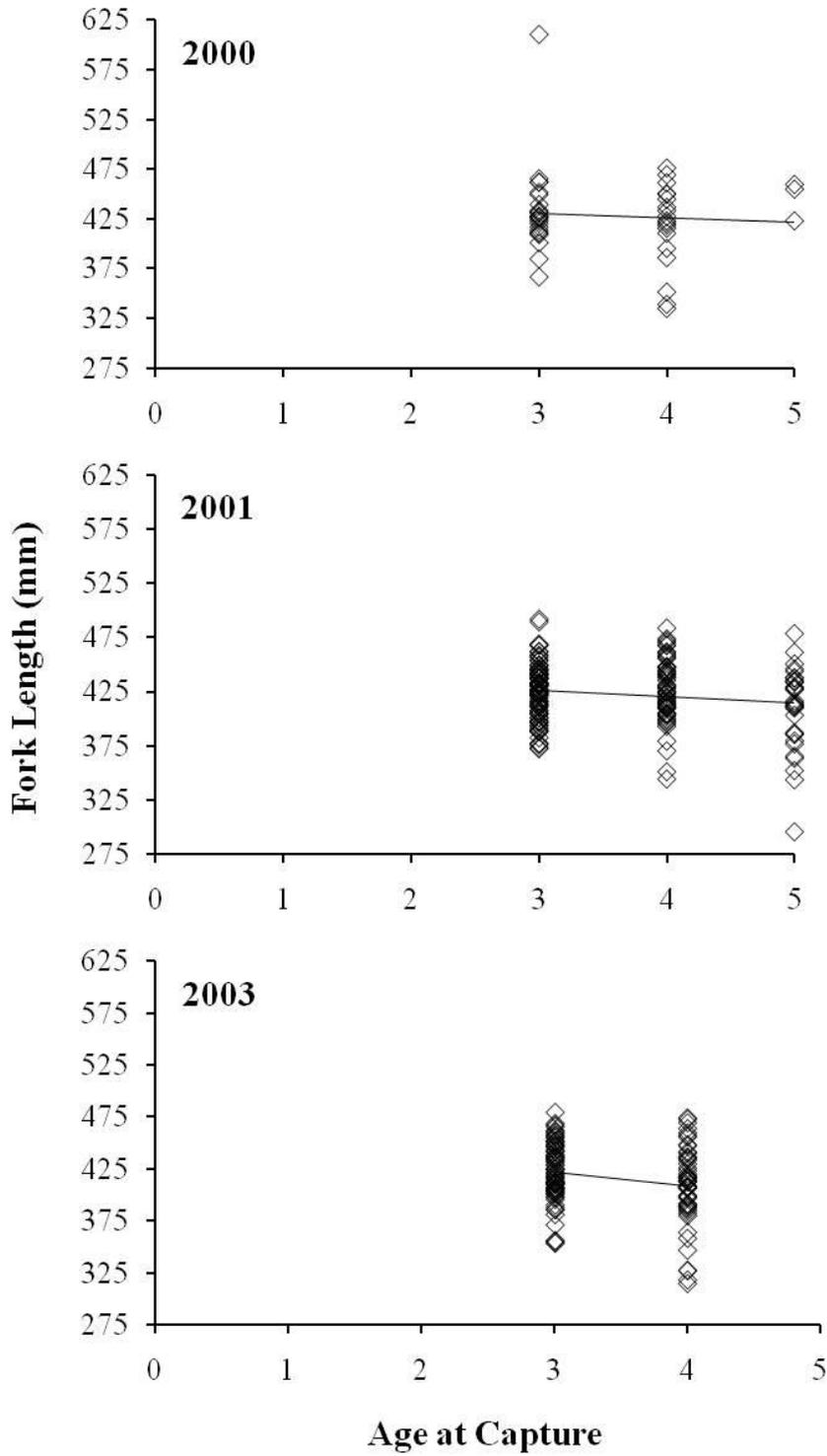


Figure 3.3 Regressions of back-calculated fork length at age 3 vs. age at capture for the 2000, 2001, and 2003 year-classes. Mean back-calculated fork length at age 3 decreases significantly as age at capture increased for the 2001 and 2003 year-classes.

Table 3.1 Results of regression analyses testing for relationships between walleye back-calculated fork length at ages 1, 2, and 3 and age at capture; x - age at capture; and y -estimated fork length at the given previous age. Significant p-values are bold-faced.

Year-Class	Age at Back-Calculation	Equation	R ²	F-value	p-value	Sample Size
2000	1	y= -7.363x+221.45	0.182	23.40	<0.001	107
	2	y= -7.880x +359.12	0.062	4.92	0.02	77
	3	y= -4.449x +443.73	0.004	0.19	0.33	46
2001	1	y= -3.081x +208.56	0.049	19.00	<0.001	368
	2	y= -5.219x +350.74	0.044	12.75	<0.001	279
	3	y= -5.919x +444.48	0.023	4.32	0.02	189
2003	1	y= -5.446x+ 188.97	0.098	33.47	<0.001	310
	2	y= -6.179x +323.65	0.030	6.84	0.005	221
	3	y= -12.414x +458.50	0.035	4.61	0.02	131

Table 3.2 Estimated size-selective mortality (a) and selection intensity (r) for all year-classes at ages 1, 2 and 3 (\pm SD); d - change in mean length of fish, in one year, within an age-group.

Year-Class	Age at back-calculation	Standard Deviation	d	a (\pm SD)	r (\pm SD)
2000	1	16.646	-7.363	-0.027 (\pm 0.015)	-0.597 (\pm 0.165)
	2	24.185	-7.880	-0.013 (\pm 0.008)	-0.440 (\pm 0.136)
2001	1	17.484	-3.081	-0.010 (\pm 0.003)	-0.238 (\pm 0.030)
	2	25.456	-5.219	-0.008 (\pm 0.004)	-0.277 (\pm 0.062)
	3	30.518	-5.919	-0.006 (\pm 0.003)	-0.262 (\pm 0.056)
2003	1	17.383	-5.446	-0.018 (\pm 0.004)	-0.423 (\pm 0.042)
	2	28.227	-6.179	-0.008 (\pm 0.002)	-0.295 (\pm 0.038)
	3	33.066	-12.414	-0.011 (\pm 0.005)	-0.506 (\pm 0.101)

CHAPTER 4: GENERAL DISCUSSION

The goals of this research were to: identify patterns of the length-at-age and growth differences of western basin Lake Erie walleye among three sub-basins of capture and four year-classes, investigate the age at the first and full recruitment to the walleye fishery, and to estimate size-selectivity mortality rate and selection intensity.

Overall, my findings suggest that:

- 1) Estimated fork length at age 1 of western basin Lake Erie walleye was similar among the western, west-central or east-central sub-basins of capture, suggesting same basin of origin (western basin);
- 2) Estimated fork length at ages 2 and 3 generally increased from west to east within the sampling areas of Lake Erie;
- 3) Walleye are likely first recruited to the recreational and commercial fisheries as early as age 1, but likely had not been fully recruited to the fishery by age 3;
- 4) Evidence of size-selective mortality was detected in ages 1, 2, and 3 walleye of the western basin Lake Erie population. Larger and faster growing fish were apparently targeted by the walleye fishery, resulting in the differential persistence of smaller and slower growing fish.

Size-selective mortality is not unique to this population. It has been found in both aquatic and terrestrial species, including Atlantic cod (Hanson and Chouinard 1992; Chen and Mello 1999; Swain et al. 2007), Pacific salmon (Ricker 1981), bluegill, pumpkinseed and yellow perch (Goedde and Coble 1981; Coble 1988), walleye (Spencer 2010),

bighorn sheep (Coltman et al. 2003), and the Himalayan snow lotus (Law and Salick 2005). Selection pressure applied by humans has been found to result in evolutionary change of morphologic traits (i.e., body size/horn size) (Ricker 1981; Coltman et al. 2003; Swain et al. 2007) and life history traits (i.e., age and/or size at maturation) (Chen and Mello 1999; Olsen et al. 2006) in many species (Jorgensen et al. 2007; Darimont et al. 2009). Further, previous studies indicate that size-selective fishing, where larger fish are targeted by fishing gear, can result in smaller size-at-age, slower growth rate, smaller size and earlier age at maturation, lower abundance and biomass (Beard & Kampa 1999; Conover and Munch 2002; Swain et al. 2007; Fenberg and Roy 2008; Conover et al. 2009). The ability for size-selective fishing to cause changes in these traits has implications for the western basin Lake Erie walleye population. Since the targeted removal of larger fish by gillnets increases the relative abundance of slow-growing fish in a population and their genes (Ricker 1981), the walleye commercial fishery is likely selecting for slower growth genotypes within the population. Additionally, size-selective pressure by recreational anglers has been found to reduce the body size of fish (i.e., bluegill, yellow perch, largemouth bass, northern pike, walleye) over a short period of time (Goedde and Coble 1981; Coble 1988; Spencer 2010). In a recent adaptive management study, minimum recreational size-limits of walleye in northern Alberta lakes were adjusted to pinpoint the cause of small, old walleye within the populations (Spencer 2010). In this study, two hypotheses were considered: a) a compensatory growth response to low harvest causing “stunting”. or b) size-selective mortality of larger walleye due to overharvesting by anglers. This study concluded that large minimum-size limits and heavy fishing pressure from anglers caused size-selective mortality of large

walleye and left a disproportionate number of smaller fish in the populations (Spencer 2010). Recreational fishing of walleye in Lake Erie may similarly contribute to selection for slower growth rate and smaller body size. The findings of Chapter 3, where smaller and slower growing fish were found to survive to older ages, are consistent with this idea. Smaller fish are relatively undesirable to both commercial fishermen and recreational anglers, and small females have lower fecundity than large individuals, which could ultimately affect the sustainability and yields in the future (Hutchings 2005). The findings from Chapter 3 and their implications highlight the importance of considering evolutionary consequences when making management plans.

Size-selective mortality can clearly cause changes to the targeted species, but this selective harvesting can affect other species as well. Shackell et al. (2009) found that a decrease in top predator (groundfish) body size from the western Scotian Shelf of the Northwest Atlantic due to size-selective harvesting likely contributed to an increase in prey biomass and may also have affected lower trophic levels. Since western basin Lake Erie walleye are a top predator and size-selectively harvested, a reduction in their body size (if one exists) will possibly alter their prey biomass and/or abundance and also influence other lower trophic levels. Our understanding of the implications of size-selective mortality of this population is limited by the short time series of this study. Thus, the consequences of size-selective harvesting of this population can only be postulated until more research has been conducted. Historical data of walleye size-at-age could be used to examine changes in body size that may have occurred prior to the present time.

The findings of this study can be used to improve the information used to estimate/model growth rates for the management of the western basin Lake Erie walleye. Currently, growth information is obtained by going to the field and collecting walleye at ages 1, 2, etc. in successive years so that in essence the same cohort is followed throughout life. However, this method only takes into account the fish that survive to following year to be sampled. The information from my study suggests that this approach may not provide an accurate growth rate because, as shown here, the larger and faster growing fish are being removed from the population, leaving smaller, slower growing fish in the population. Therefore, the method currently used to base growth rates solely on observed catches likely underestimates the true mean growth rate of Lake Eries western basin walleye population. These inaccuracies could ultimately affect recruitment estimates. This study can be used to derive the true growth rate and more accurately model growth within this population.

There are several possibilities to continue this research. This study found a negative relationship between estimated fork length at ages 1, 2 or 3 and age at capture, indicating that smaller and slower growing walleye are differentially surviving to older ages. However, changes in mean size-at-age were not examined. Future research should expand upon this finding and evaluate a longer time series to test if size-at-age is declining over time and if other consequences of size-selective mortality are occurring. To better understand the impact of commercial and recreational fisheries on the western basin walleye population, future studies should attempt to relate fishing mortality to estimated size-selective mortality to see if a clear pattern emerges. Will a specific amount of fishing mortality consistently produce the same size-selective mortality

estimate? If such a pattern was found and an acceptable level (if one exists) of size-selective mortality was set for a population, managers could use this information to help set fishing harvest quotas and control the estimated fishing mortality associated with these quotas to ensure that fishing activities will not alter mean size-at-age of the population. If this management approach is successful, it could be expanded to other fisheries worldwide. Spencer (2010) showed that tag limits could be effectively used to produce the desired growth rates and sizes within a population. However, the effectiveness of this approach was limited by angler compliance; if the regulations were ignored, the plan will no longer produce the desired outcome.

Additionally, my study did not differentiate between sexes. Future studies should consider looking at differences in size-selective mortality between male and female fish. After age 3, western basin walleye growth rate differs between genders; female walleyes grow faster than males (Zhao 2005). If females grow faster than males from birth, they likely become vulnerable to fishing gears sooner than male walleyes; are females experiencing more size-selective pressure than males? Over time, how will this affect the fecundity, abundance and mean size-at-age of the population (if it hasn't already)? Size-selective mortality of the population should receive continued study to monitor long term effects because genetic based effects of size-selective mortality may not be easily reversible (Law 2000).

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