

CHARACTERIZATION OF A DISTINCT POPULATION OF LAKE TROUT
IN ELK LAKE (ANTRIM COUNTY), MICHIGAN

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ABSTRACT

CHARACTERIZATION OF A DISTINCT POPULATION OF LAKE TROUT IN ELK LAKE (ANTRIM COUNTY), MICHIGAN

by Laura Mathews

Elk Lake is a mid-sized inland lake located in Antrim County, Michigan. The lake was hydrologically separated from Lake Michigan during the mid 19th century and contains a self-sustaining population of Lake Trout (*Salvelinus namaycush*). Elk Lake Lake Trout display unique life history and spawning characteristics relative to hatchery fish stocked in Lake Michigan. Observations indicate that the Lake Trout in Elk Lake may spawn in deep water, suggesting that these may be a remnant of populations extirpated from the Great Lakes. The objectives of this study were to estimate the abundance of Lake Trout in Elk Lake and determine defining characteristics of the population by comparisons of morphometry and growth between Lake Trout from Elk Lake, stocked lean forms from Lake Michigan, and lean forms from Lake Superior.

It was determined that Lake Trout from Elk Lake are morphologically different than forms of Lake Trout from Lake Michigan and Lake Superior; Elk Lake Lake Trout have a leaner body form than the other populations. The morphometric differences and the fact they are genetically different from strains currently stocked in Lake Michigan support the hypothesis that they may be a remnant population of extirpated Great Lakes Lake Trout. In addition, the Elk Lake Lake Trout have higher overall growth rates ($L_{\infty, \text{age } 4-11} = 669 \text{ mm}$; $k_{\text{age } 4-11} = 0.35$) than the lean forms from Lake Superior ($L_{\infty, \text{age } 4-11} = 620 \text{ mm}$; $k_{\text{age } 4-11} = 0.18$) and Lake Michigan ($L_{\infty, \text{age } 4-11} = 779 \text{ mm}$; $k_{\text{age } 4-11} = 0.24$), however after age 5 the Elk Lake Lake Trout growth rates are surpassed by Lake Trout from Lake Michigan. The population of Lake Trout in Elk Lake was estimated at 1,001 fish ($\sigma^2 = 16,748$; 95% CI=749-1255 fish) for ages 2 to 11.

Due to the ability to maintain a self-sustaining population, the Elk Lake Lake Trout may be a viable source for stocking the Great Lakes, but future research should continue to define characteristics of this population to determine if they are a remnant form of native Great Lakes Lake Trout.

TABLE OF CONTENTS

LIST OF FIGURESvi

CHAPTER

I. MORPHOMETRIC COMPARISION BETWEEN LEAN FORMS OF LAKE TROUT FROM ELK LAKE (ANTRIM COUNTY), MI, LAKE MICHIGAN, AND LAKE SUPERIOR 1

Introduction 1

Methods 4

Results 10

Discussion 16

 LITERATURE CITED..... 19

II. POPULATION CHARACTERISTIC COMPARISION BETWEEN LEAN LAKE TROUT FROM ELK LAKE (ANTRIM COUNTY), MI, LAKE MICHIGAN, AND LAKE SUPERIOR 25

Introduction 25

Methods 25

Results 30

Discussion 34

 LITERATURE CITED..... 37

APPENDICES 40

LIST OF FIGURES

FIGURE

1. Elk Lake, Antrim County, Michigan. Elk Lake is the final lake in the Chain of Lakes waterway. The waterway spans 120 km and encompasses 14 inland lakes, including Lake Skegemog and Torch Lake, which drain into Elk Lake. Waterways are colored white while land is colored gray. The contour lines represent 10 m and demonstrate the steep slope and maximum depth of 61m in Elk Lake. 6

2. Truss measurements used in the analysis. F1-F31 are truss measurements described in Moore and Bronte (2001), while T1, T9, T13, T16, T21, T25, T28, T29, T30, T31 are additional truss measures added to increase the accuracy of the measurements. 8

3. Example image of Elk Lake Lake Trout used for the geometric analysis. The lines indicate 20% (A), 30% (B), 40% (C), and 50% (D) of the standard length (E). The 20 landmarks indicate the 20 homologous features used to distinguish the morphological differences between the Lake Trout from Elk Lake, lean forms from Lake Superior, and stocked lean forms from Lake Michigan. 10

4. Figure 4. Results of the discriminate function analysis for the morphometric truss analysis representing the variation in shape among Lake Trout from Elk Lake (triangle), Lake Michigan (square), and Lake Superior (circle). Lake Trout from Lake Superior had smaller head measurements than individuals from Elk Lake and Lake Michigan. Lake Trout from Elk Lake had smaller mid-body measurements than individuals from Lake Michigan..... 11

5. Truss measurements that were negatively correlated with axis LD1 in the discriminate function analysis are shown in thick black lines (a). Lake Superior Lake Trout head measurements were smaller than measurements of Elk Lake and Lake Michigan Lake Trout. Truss measurements negatively correlated with axis LD2 in the discriminate function analysis are shown in thick black lines (b). Elk Lake Lake Trout had a narrower and more compressed mid bodies than individuals from Lake Michigan. The fish shown are from Elk Lake. 12

6. Results of the discriminate function analysis for the morphometric geometric analysis representing the variation in shape among Lake Trout from Elk Lake (triangle), Lake Michigan (square), and Lake Superior (circle) 14

7. Deformation grids showing shape differences (at 3x magnification) described by regressing the linear discriminant 1 axis values against the partial warp scores between Lake Trout from (a) Elk Lake, (b) Lake Michigan, and (c) Lake Superior. Lines were added between landmarks (1-20) to ease visualization of differences. 15

8. Deformation grids showing shape differences (at 3x magnification) described by regressing the linear discriminant 2 axis values against the partial warp scores for Lake Trout from (a) Elk Lake, (b) Lake Michigan, and (c) Lake Superior. Lines were added between landmarks (1-20) to ease visualization of differences	16
9. Age frequencies of Lake Trout from Elk Lake, Michigan, sampled during the 2009-2012 sampling seasons.	32
10. Mean length-at-age (mm) of Lake Trout from Elk Lake, Michigan (back-calculated; circles), and Lake Michigan (measured; triangles), and Lake Superior (measured; squares)	32
11. Von Bertalanffy model estimates for Lake Trout from Elk Lake, Michigan (solid line), and Lake Michigan (dotted line), and Lake Superior (dashed line). Models were estimated from back-calculated lengths in Elk Lake and observed values from Lake Michigan and Lake Superior	33

CHAPTER I

MORPHOMETRIC COMPARISON BETWEEN LEAN FORMS OF LAKE TROUT FROM ELK LAKE (ANTRIM COUNTY), MI, LAKE MICHIGAN, AND LAKE SUPERIOR

Introduction

Phenotypic diversity is present to varying degrees in many species, and differences can be expressed as resource polymorphisms or the occurrence of many morphotypes in a population that use different resources (Andersson et al. 2007). Phenotypic plasticity is described as environmentally caused variation in the development of an organism (Alpert and Simms 2002; West-Eberhard 1989) and encompasses all types of phenotypic variation due to the environment (Stearns 1989). Resource polymorphisms result in variations in color, size, shape, behavior, or life history traits, and often are represented by more than one factor (Smith and Skúlason 1996). These differences in morphology are often driven by phenotypic plasticity and genetic differences (Andersson et al. 2007; Nordeng 1983; Gislason et al. 1999) and can occur when there are underutilized resources (Kahilainen and Ostbye 2006; Smith and Skúlason 1996), competition (Svanbäck et al. 2008), and predation (Lima and Dill 1990) or when changing abiotic factors make individual traits suited for the previous environment no longer compatible with the new environment (Whitman and Agrawal 2009). In aquatic systems, phenotypic differences are common in freshwater and anadromous species and in small landlocked lakes (Smith and Skúlason 1996).

Morphometry represents the quantitative description, analysis, and interpretation of form and structure of an organism (Rohlf 1990). Differences of morphometric measures can be the result of many factors, including competition between or within species (Robinson and Wilson 1994), anthropogenic habitat alteration (Franssen 2011), diet, and nutrition (Wimberger 1992).

Morphological variations in fish are typically represented by differences of shape and size of fins, body and head depth, or in the structure of the stomach and gut (Skúlason and Smith 1995). Examples of morphometric differentiation in fish species are exemplified by sympatric morphotypes of Lake Whitefish (*Coregonus clupeaformis*), referred to as dwarf and normal, found in the St. John River drainage in Maine, Quebec, and Ontario (Pigeon et al. 1997). The two forms display differences in their growth, maturity, morphology (Fenderson 1964), and genetics (Kirkpatrick and Selander 1979). Similarly, Arctic Charr (*Salvelinus alpinus*) display great morphometric variability among regions (Jonsson and Jonsson 2001; Smith and Skúlason 1996; Chavarie et al. 2013) including differences in feeding ecology, morphology, reproduction, often spawning in different locations or at different times (Jonsson and Jonsson 2001), and adult body size (Smith and Skúlason 1996). Some of these morphometric and life history differences are large enough that misidentification as different species is possible (Chavarie et al. 2013).

Lake Trout (*Salvelinus namaycush*) are a relatively long-lived species (Eshenroder et al. 1995) and represent considerable genetic diversity (Burnham-Curtis et al. 1995; Krueger and Ihssen 1995). The evolutionary biology of Lake Trout in their native range throughout North American and Canada was strongly influenced by glaciation during the Pleistocene epoch (Eshenroder et al. 1995; Wilson and Mandrak 2004), and a close relationship exists between the present distribution of Lake Trout and glaciated areas (Lindsey 1964). During the four to twenty glaciation cycles that occurred during the Pleistocene epoch, Lake Trout cycled through colonization of refugial habitats and retreat and extirpation (Eshenroder et al. 1995; Wilson and Mandrak 2004). Despite the process of colonization and retreat, Lake Trout have maintained genetic (Krueger and Ihssen 1995) and phenotypic diversity among forms and populations until the mid-20th century.

Lake Trout recolonized the Great Lakes after the Pleistocene epoch (Christie 1974) and remained abundant until the first half of the 20th century when overexploitation, habitat degradation, and Sea Lamprey (*Petromyzon marinus*) predation decimated populations (Holey et al. 1995; Hansen 1999). Since this time, efforts to reestablish Lake Trout populations include Sea Lamprey control, fishing regulations, and yearly stocking of hatchery fish (Page et al. 2004; Perkins and Krueger 1995). Hatchery fish have increased the number of mature Lake Trout in the Great Lakes (Marsden et al. 1995), however full Lake Trout restoration has not yet been realized (Guinand et al. 2003).

Prior to their decline, Lake Trout populations in the Great Lakes consisted of many morphological forms associated with deep or shallow water (Hansen 1999; Krueger and Ihssen 1995; Holey et al. 1995). In Lake Michigan, forms included lean forms associated with shallow water (Brown et al. 1981, Holey et al. 1995) and siscowet like forms associated with deep water (Krueger and Ihssen 1995). Deep water Lake Trout in Lake Michigan were believed to spawn in 50-85 m water depth on clay, gravel, and limestone and were smaller with higher fat content than shallow water trout (Holey et al. 1995). The Bay Trout, a lean deep water form found exclusively in the Green Bay area of Lake Michigan, spawned over sand, gravel, or mud in deeper water up to ten days later than the shallow water forms in the region (Holey et al. 1995). Deep water habitats were of historical importance to native Lake Trout, with commercial catch reports suggesting that two-thirds of the historical Lake Trout catch spawned at offshore sites (Dawson et al. 1997).

While historical forms of Lake Trout spawned in a variety of habitats, the majority of stocked Lake Trout in the Great Lakes spawn primarily on shallow, nearshore reefs (Marsden et al. 1995). The loss of deep water spawning strains may contribute to the current lack of

spawning variation (Marsden et al. 1995), resulting in populations of hatchery fish with fewer rare alleles than historical forms (Wilberg et al. 2003). Management and restoration of Lake Trout are currently shifting from focusing on shallow, near-shore forms to deep water forms because of the historical importance of deep reefs for native Lake Trout (Janssen et al. 2007). Presently, Lake Superior is the only Great Lake that has retained some of the historic variation of Lake Trout populations. This includes the siscowet form, a lean form found in less than 80 m of water, and a humper form primarily found in > 90 m of water with an intermediate fat level relative to the lean and siscowet forms (Eschmeyer and Phillips 1965; Moore and Bronte 2001).

Lake Trout found in Elk Lake, Michigan, display unique life history and spawning characteristics relative to the hatchery fish stocked in Lake Michigan. Elk Lake is a deep inland lake separated from Lake Michigan by a dam at Elk Rapids, Michigan. Lake Trout appear to spawn in deep water, and may be a remnant population of the extirpated Great Lakes Lake Trout. The purpose of this research was to define physical characteristics of Lake Trout in Elk Lake. To accomplish this, morphometric comparisons were made among Elk Lake Lake Trout, lean forms of Lake Trout from Lake Superior, and stocked lean forms of Lake Trout from Lake Michigan.

Methods

Study Site

Sampling was conducted in Elk Lake, Antrim County, Michigan (Figure 1). Elk Lake is a small, inland lake approximately 14.4 km in length and 3.2 km wide at its widest point with a maximum depth of 61 m and primarily clay substrate (Scott 1921). Elk Lake is the final lake in the chain of lakes watershed that spans Antrim, Charlevoix, Grand Traverse, and Kalkaska

Counties, Michigan (Figure 1). Elk Lake was once connected to Lake Michigan through Grand Traverse Bay but was hydrologically separated when a dam was installed in 1856 (Scott 1921). Elk Lake was stocked with Marquette strain Lake Trout, a remnant wild population from Lake Superior (Bronte et al. 2007) during the early 1970's. Recent genetic analysis has shown the Elk Lake population is genetically different from any form stocked into Lake Michigan or Elk Lake, including the Marquette strain, and lean forms from Lake Superior (Michigan State University; Dr. Kim Scribner, unpublished data).

Field Sampling

Adult Lake Trout were captured in Elk Lake with trap nets (1.8 m wide x 152.4 m long with 6.4 cm mesh) in fall and spring 2009 and bottom gill nets (6 m wide x 900 m long with 7.6 cm mesh) in fall and spring of 2009, 2011, and 2012. During spring 2009, trap nets (n=13) and bottom gill nets (n=4) were set in waters depths of <7.6 m and >30.5 m, respectively. In fall 2009, bottom gill nets (n=4) were set in water depths <18.3 m, while two bottom gill nets were set at depths 18.3-40 m. During fall 2011, 69 bottom gill nets were set in the western side of Elk Lake in water depths 24.4-60 m for one hour sets to decrease the risk of mortality and by-catch. In spring 2012, 44 bottom gill nets in water depths 24.4-60 m were set primarily on the northern and western portions of the lake. During fall 2012, 75 bottom gill nets were set in depths ranging from 24.4-60 m.

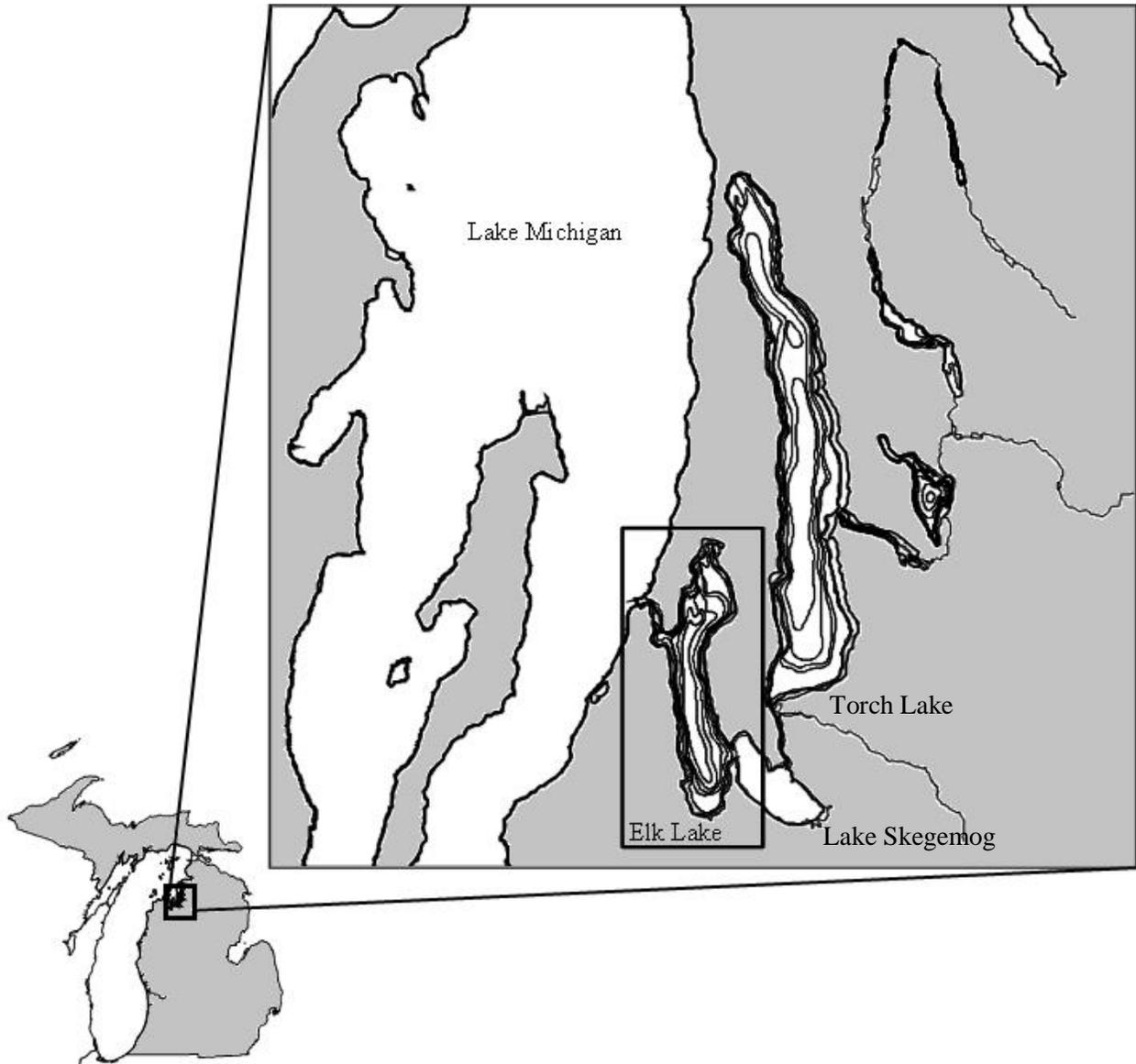


Figure 1. Elk Lake, Antrim County, Michigan. Elk Lake is the final lake in the Chain of Lakes waterway. The waterway spans 120 km and encompasses 14 inland lakes, including Lake Skegemog and Torch Lake, which drain into Elk Lake. Waterways are colored white while land is colored gray. The contour lines represent 10 m and demonstrate the steep slope and maximum depth of 61m in Elk Lake.

Once captured, an image of each individual Lake Trout was taken following the protocol established in Muir et al. (2012). Images were captured using a Canon PowerShot D20 water proof digital camera. The camera was positioned on a horizontal manfrotto tripod 1-m above each fish. A mesh cradle bordered by two rulers for calibration was used to hold the fish and

create a planar surface relative to the camera lens. Each Lake Trout was aligned from the tip of the snout to the center of the caudal fin to a black line on the inside of the cradle under the mesh. Utensils were used to ensure that the mouth and operculum were closed, dorsal and anal fins were extended, and pectoral and pelvic fins were parallel to the body on all individuals.

Lake Trout were collected in Lake Michigan in bottom gill nets set for 24 hour periods during summer and fall 2012. Six bottom gill nets were set at water depths of 24.4-60 m in Grand Traverse Bay during July 2012 and in southern Lake Michigan near Saugatuck during September 2012. Images were taken and the length was recorded for each individual fish following the same methods described above. In Lake Superior, Lake Trout were collected using bottom gill nets near Isle Royal. Images of lean Lake Trout from Lake Superior were provided by Andrew Muir (Great Lakes Fishery Commission) for comparative purposes.

Morphometric Truss Analysis

Images from Elk Lake (n=201), Lake Michigan (n=204), and Lake Superior (n=55) were analyzed using the protocol described in Moore and Bronte (2001) with 31 truss elements from 14 landmarks (Figure 2). An additional 11 truss measurements were added to the outline of the fish to increase accuracy linear measures that might be influenced by the curvature of the body (Figure 2). Landmarks were placed on the digital images, and truss elements were measured using Image Pro Plus 5.1 software. Measurements were standardized for size variation between individuals by dividing each truss element by the total sum of truss elements for each individual fish. A multivariate analysis of variance was completed to determine if differences existed between the groups using R (R Core Development Team, 2011). Discriminate function analysis determined which truss elements explained the greatest amount of variation among the groups. Functions were then tested to determine if individuals could be correctly re-classified (i.e., Elk

Lake, Lake Michigan, or Lake Superior) based on the identified truss elements. Truss elements where $r > |0.5|$ were considered correlated and responsible for the variation between the groups.

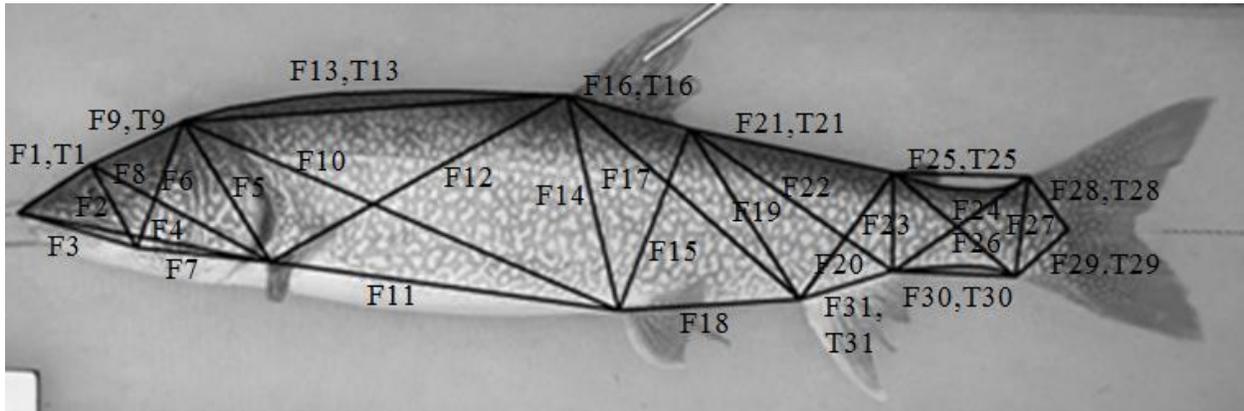


Figure 2. Truss measurements used in the analysis. F1-F31 are truss measurements described in Moore and Bronte (2001), while T1, T9, T13, T16, T21, T25, T28, T29, T30, T31 are additional truss measures added to increase the accuracy of the measurements.

Morphometric Geometric Analysis

The morphology of lean Lake Trout from Elk Lake, Lake Michigan, and Lake Superior was also evaluated using geometric analysis according to protocols defined in Zimmerman et al. (2012) and Parsons et al. (2003). A grid was digitally superimposed on each image beginning at the tip of the snout and ending at the midpoint of the hypural plane with lines indicating 20%, 30%, 40%, and 50 % of the individual's standard length with a horizontal line indicating the midpoint of the grid (Figure 3). The grid was then oriented so the lateral line of the fish aligned with the midline. Images where the midline could not be aligned were eliminated, reducing the sample size for analysis (Elk Lake, $n=49$; Lake Michigan, $n=66$; Lake Superior, $n=62$). The program, TPS Util, was used to create TPS files that were then imported into TPS Dig, a program available on the State University of New York at Stony Brook morphometric website (<http://life.bio.sunysb.edu/morph/>; Figure 3) where coordinates for 20 landmarks were digitized. The program TPS relW was used to perform a generalized procrustes analysis on the coordinates

which centers all of the specimens then scales and rotates the images to a common size and orientation (Parsons et al. 2003; Zimmerman et al. 2006). A consensus form, or the mean coordinates for each landmark averaged across all of the specimens, was determined and compared against the landmarks (Parsons et al. 2003), resulting in a weight matrix that contained 17 partial warp scores. The partial warp scores produced relative differences in shape among the groups by describing the differences of each specimen to the consensus form (Parsons et al. 2003; Zimmerman et al. 2006). The partial warp scores were evaluated using discriminate function analysis to generate re-classification functions, which were then tested to determine if individuals could be correctly re-classified (i.e., Elk Lake, Lake Michigan, or Lake Superior) based on their shape. The program TPSRegr was used to construct deformation grids to visualize shape differences among the groups (i.e., Elk Lake, Lake Michigan, or Lake Superior) by regressing the linear discriminant axis values against the partial warp scores for each lake separately.

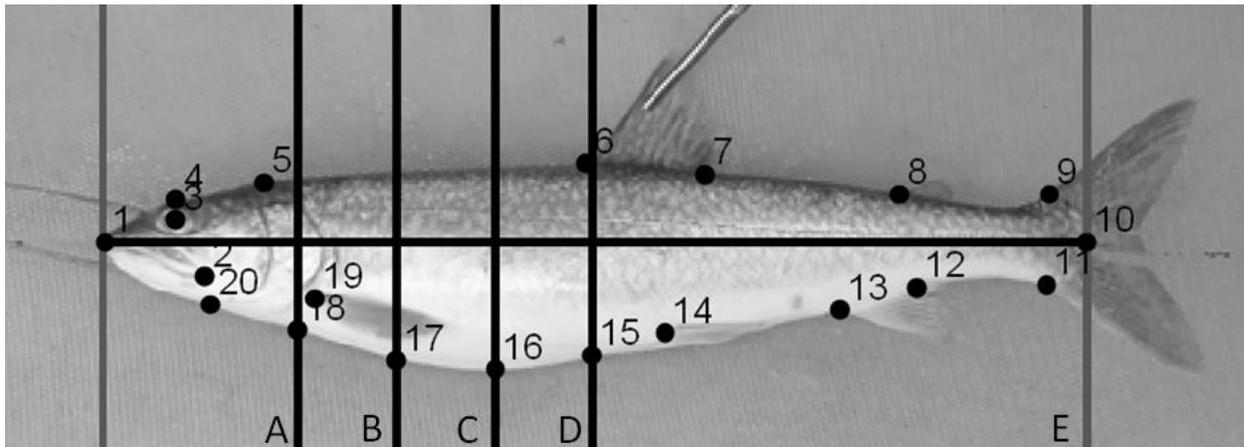


Figure 3. Example image of Elk Lake Lake Trout used for the geometric analysis. The lines indicate 20% (A), 30% (B), 40% (C), and 50% (D) of the standard length (E). The 20 landmarks indicate the 20 homologous features used to distinguish the morphological differences between the Lake Trout from Elk Lake, lean forms from Lake Superior, and stocked lean forms from Lake Michigan.

Results

Morphometric Truss Analysis

The Elk Lake Lake, Lake Michigan, and Lake Superior Lake Trout were morphometrically different from one another ($F_{2,457}=17.4$, $P<0.0001$). The discriminate function analysis axis LD1 described 54% of the variation (Figure 4), while axis LD2 was responsible for 46% of the variation. Individual fish from Lake Superior had smaller head measurements than individual Lake Trout from Elk Lake and Lake Michigan, which were similar to one another. Individuals from Elk Lake had smaller mid-body measurements than individuals from Lake Michigan. Truss measurements associated with the head region were negatively correlated with LD1 (Figure 5: F6, $r=-0.52$; F9, $r=-0.58$; T9, $r=-0.58$). Lake Superior individuals had smaller head measurements than individuals from Elk Lake and Lake Michigan, which were similar in head measurements. Measurements associated with the mid-body region were negatively correlated with LD2 (Figure 5: F10, $r=-0.55$; F11, $r=-0.63$; F12, $r=-0.65$; F13, $r=-0.56$; F14, $r=-0.60$; F15, $r=-0.51$; F17, $r=-0.50$; F19, $r=-0.50$; F23, $r=-0.57$; T13, $r=-0.56$). LD2 separated individuals from Elk Lake as having smaller and compressed mid-body regions than individuals from Lake Michigan. Ninety-two percent of Lake Trout from Elk Lake were correctly classified as originating from Elk Lake, 97% of individuals from Lake Michigan were classified correctly as originating from Lake Michigan, and 92% of individuals from Lake Superior were correctly classified as originating from Lake Superior.

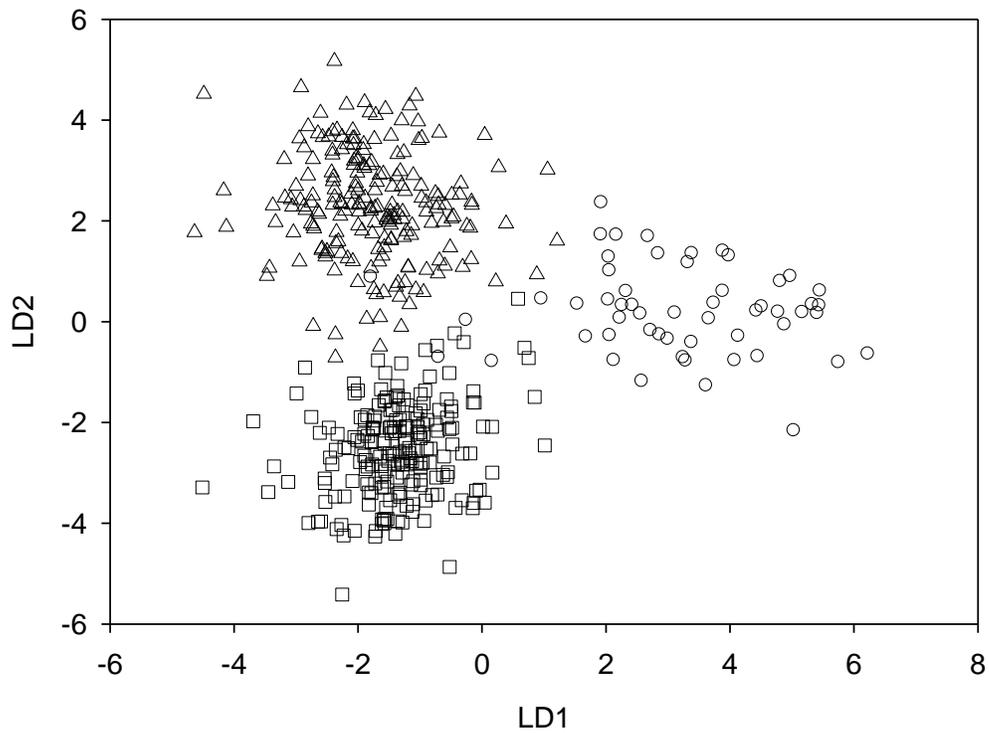


Figure 4. Results of the discriminate function analysis for the morphometric truss analysis representing the variation in shape among Lake Trout from Elk Lake (triangle), Lake Michigan (square), and Lake Superior (circle). Lake Trout from Lake Superior had smaller head measurements than individuals from Elk Lake and Lake Michigan. Lake Trout from Elk Lake had smaller mid-body measurements than individuals from Lake Michigan.

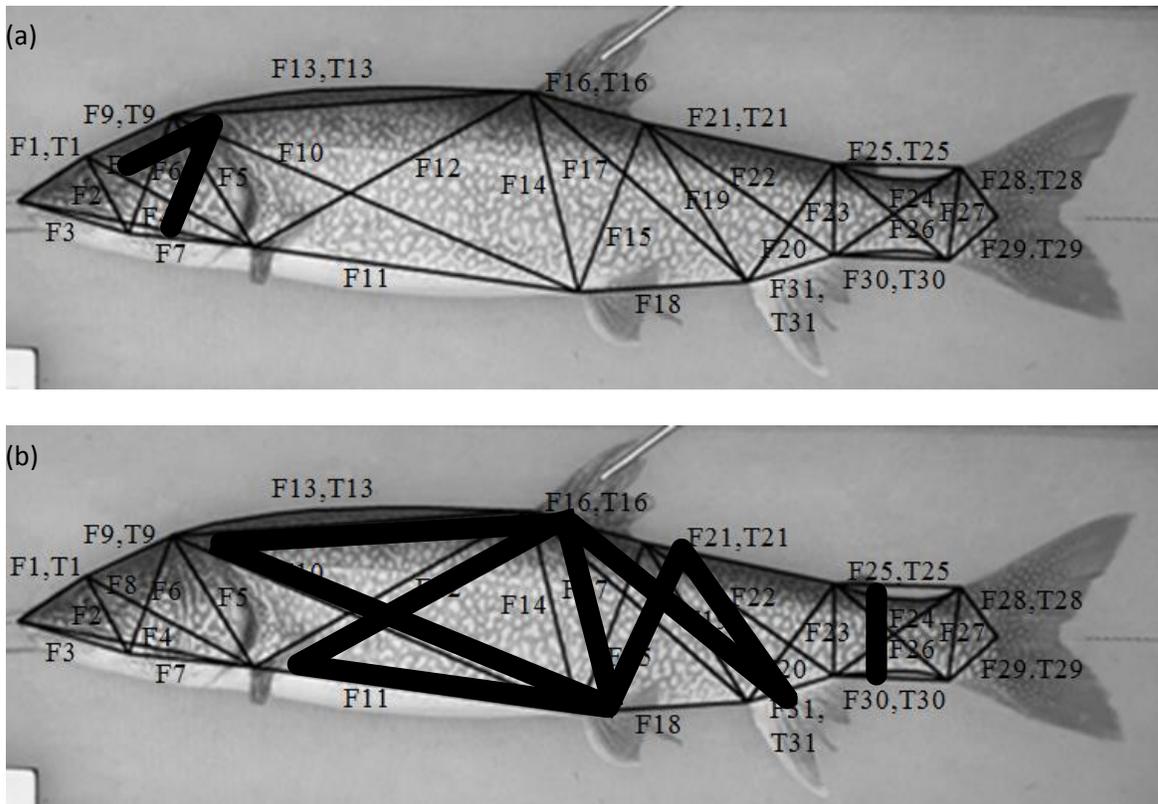


Figure 5. Truss measurements that were negatively correlated with axis LD1 in the discriminate function analysis are shown in thick black lines (a). Lake Superior Lake Trout head measurements were smaller than measurements of Elk Lake and Lake Michigan Lake Trout. Truss measurements negatively correlated with axis LD2 in the discriminate function analysis are shown in thick black lines (b). Elk Lake Lake Trout had a narrower and more compressed mid bodies than individuals from Lake Michigan. The fish shown are from Elk Lake.

Morphometric Geometric Analysis

Differences in morphology among the three Lake Trout morphotypes were also detected with the geometric analysis. Sixty three percent of the variation among the groups was accounted for by axis LD1, while axis LD2 described 37% of the variation (Figure 6). Overall, 90% of individuals from all three populations were classified correctly. In reassessment tests, individuals from Elk Lake were classified correctly 84% of the time; Lake Michigan, 91% of the time; and Lake Superior, 94% of the time.

Deformation grids were created to depict shape differences among the three populations (Figure 7; Figure 8). Elk Lake Lake Trout had a more elongated and narrow head region when compared with fish from Lake Michigan and Lake Superior, while Lake Michigan and Lake Superior were more similar in head shape (Figure 7; Figure 8; landmarks 1-5). Elk Lake has a more upturned head than Lake Michigan and Lake Superior (Figure 8). Body depth was the greatest differentiating feature between Elk Lake Lake Trout and Lake Trout from Lake Michigan and Lake Superior. Elk Lake fish were more compressed, elongated, and fusiform in shape when compared to the other two populations, which were broader in the mid-body region (Figure 7; Figure 8; landmarks 6,7,14,15,16,17). The caudal area of Elk Lake Lake Trout was relatively narrower and the adipose fin was set back further aligning with the anal fin posterior insertion (Figure 7; Figure 8; landmarks 8,12). In contrast, Lake Michigan and Lake Superior fish were more similar with a wider caudal peduncle. The adipose fin was forward of the posterior insertion point of the anal fin for the Lake Michigan and Lake Superior Lake Trout relative to Lake Trout from Elk Lake.

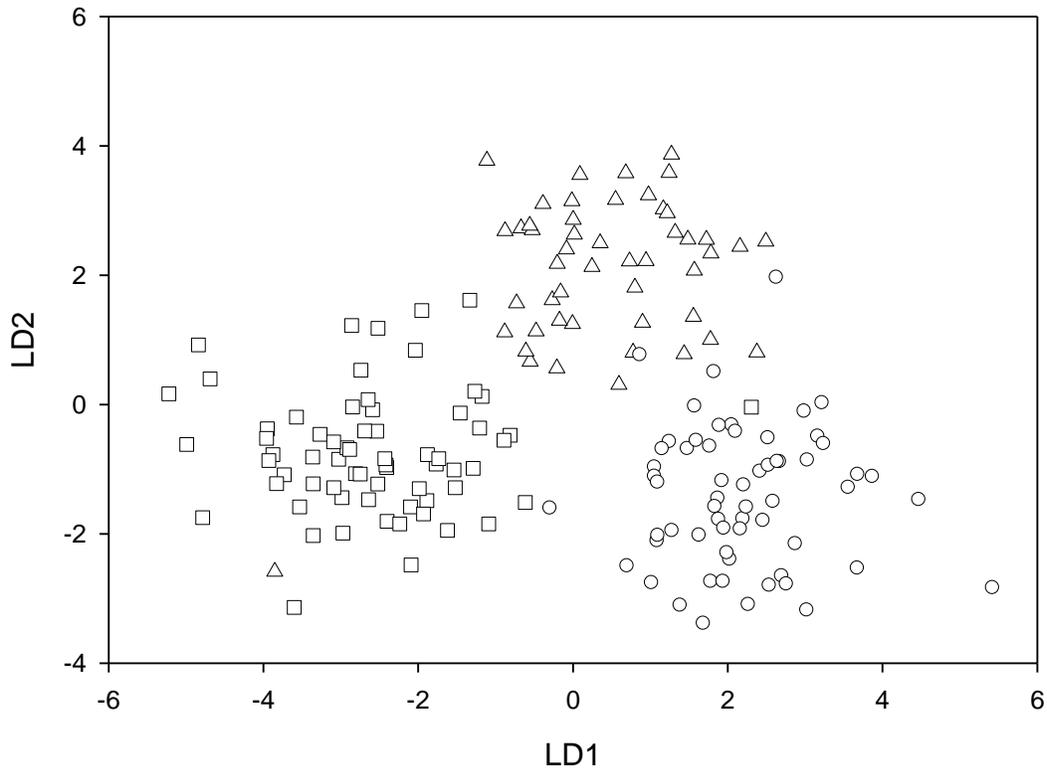


Figure 6. Results of the discriminate function analysis for the morphometric geometric analysis representing the variation in shape among Lake Trout from Elk Lake (triangle), Lake Michigan (square), and Lake Superior (circle).

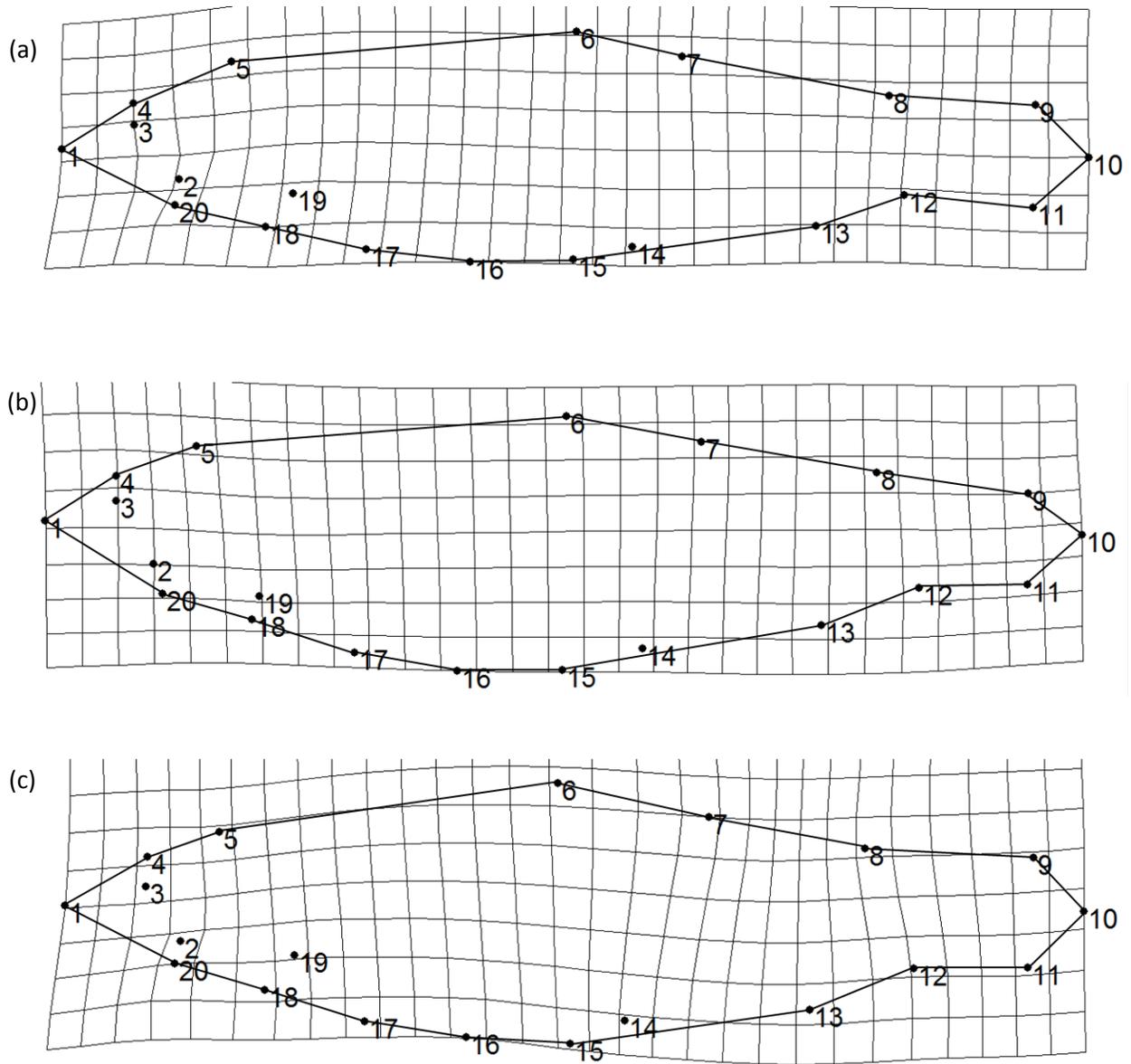


Figure 7. Deformation grids showing shape differences (at 3x magnification) described regressing the linear discriminant 1 axis values against the partial warp scores for Lake Trout from (a) Elk Lake, (b) Lake Michigan, and (c) Lake Superior. Lines were added between landmarks (1-20) to ease visualization of differences.

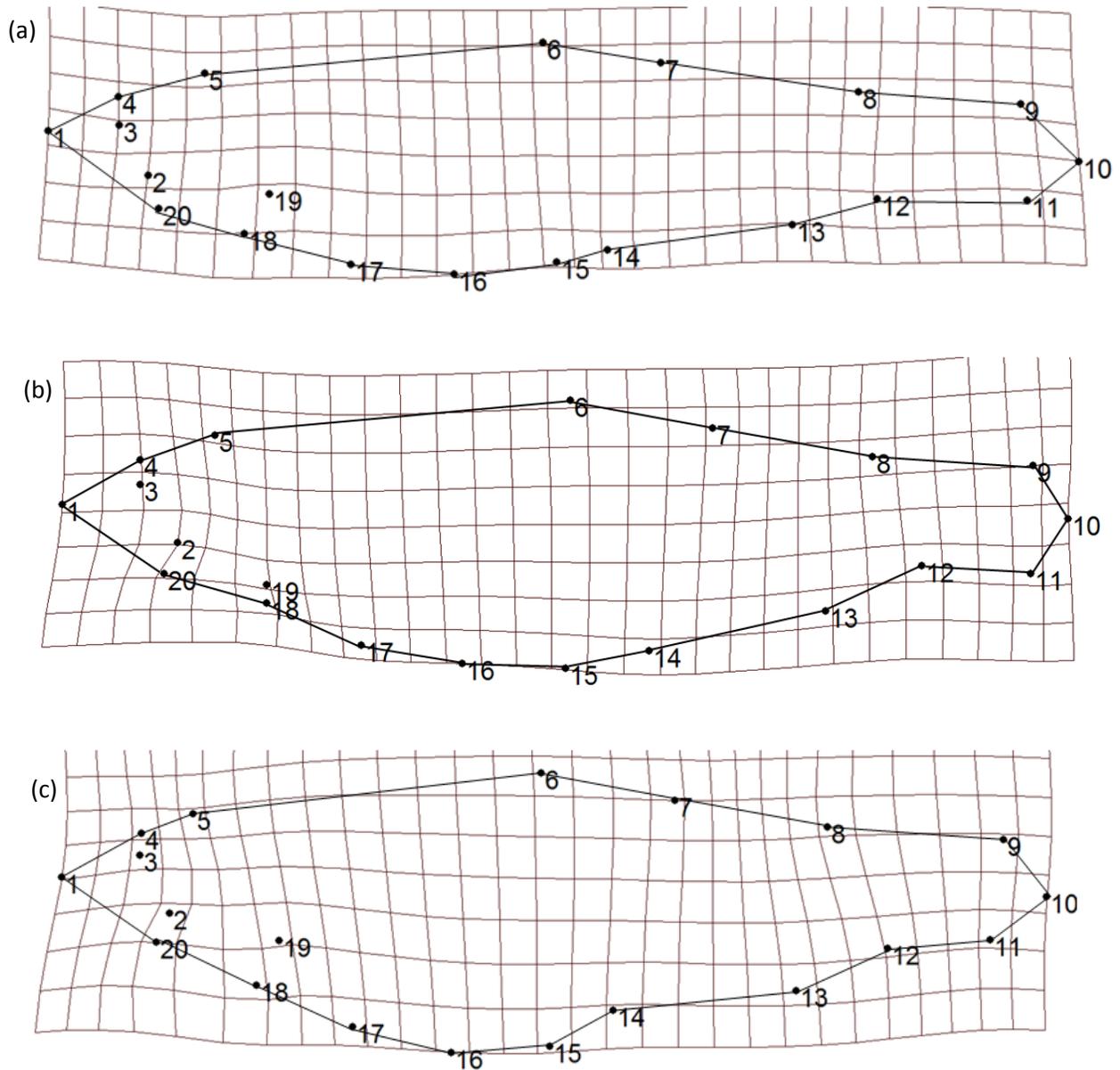


Figure 8. Deformation grids showing shape differences (at 3x magnification) described by regressing the linear discriminant 2 axis values against the partial warp scores for Lake Trout from (a) Elk Lake, (b) Lake Michigan, and (c) Lake Superior. Lines were added between landmarks (1-20) to ease visualization of differences.

Discussion

Lake Trout from Elk Lake are morphologically different than forms from Lake Michigan and lean forms from Lake Superior. Typically, intraspecific differences in morphology, life

history, and behavior reflect differences in both diet and habitat (Chavarie et al. 2013). In both Lake Superior and Great Slave Lake, Lake Trout populations have partitioned resources by habitat and depth (Chavarie et al. 2013; Zimmerman et al. 2009). Lean forms of Lake Trout found primarily in shallow water (<50 m) typically are piscivorous (Fisher and Swanson 1996; Zimmerman et al. 2009). Deep-water Lake Trout are believed to have adapted deep-water feeding strategies to avoid competition with lean (shallow-water) forms (Eshenroder 2008), and typically feed on deep-water ciscoes (Zimmerman et al. 2009). Lake Trout from Elk Lake are most similar in body shape to lean forms, yet seem to display behaviors similar to deep-water forms. Unlike Lake Superior where competition with other forms resulted in different feeding patterns (Eshenroder 2008; Zimmerman et al. 2009), only one form of Lake Trout appears to exist in Elk Lake. Lake Trout from Elk Lake have developed a deep-water feeding strategy utilizing Cisco (*Coregonus artedi*) and Deep-Water Sculpin (*Myoxocephalus thompsonii*) in their diets (Michigan Department of Natural Resources; Jory Jonas, unpublished data). Elk Lake Lake Trout are found primarily in deep water, through much of the year including the fall spawning season (Michigan Department of Natural Resources; Jory Jonas, unpublished data). If Elk Lake fish are spawning in deep water, similar to historic forms of native Great Lakes Lake Trout (Dawson et al. 1997, Holey et al. 1995), it is likely over a clay bottom, similar to native forms of Lake Michigan Lake Trout (Marsden et al. 1995).

Both the truss and geometric analysis resulted in similar patterns of morphological differences among the Elk Lake, Lake Michigan, and Lake Superior Lake Trout populations. Similar to other studies (Adams and Rohlf 2000; Parsons et al. 2003), the geometric analysis provided greater discriminatory power among the groups. We were better able to distinguish head, body, and caudal region shape differences between the Elk Lake population and the other

populations with the geometric analysis. In addition, we observed that the Lake Michigan and Lake Superior populations appear more similar in body and head shape compared to the Elk Lake population. Although both techniques are valid in determining morphological differences that exist between populations, the geometric analysis is a better tool for describing morphological differences (Parsons et al. 2003).

The Lake Trout population in Elk Lake is either a separate and distinct form or may be a remnant of now extirpated native Lake Michigan Lake Trout. This hypothesis is supported by both the morphometric information presented here and previous genetic analysis, which demonstrated that Elk Lake Lake Trout were genetically different from strains currently stocked in Lake Michigan (including the Marquette strain) and lean forms from Lake Superior (Michigan State University; Dr. Kim Scribner, unpublished data). Due to its ability to maintain a self-sustaining population, the Elk Lake Lake Trout may be a viable source to re-introducing lost diversity via stocking in the Great Lakes. However, we need to better understand the population biology, behavioral ecology, and genetics of these fish before such efforts are initiated.

LITERATURE CITED

- Adams, D. C., and F. J. Rohlf. 2000. Ecological character displacement in *Plethodon*: biochemical differences found from a geometric morphometric study. Proceedings of the National Academy of Sciences 97: 4106-4111.
- Alpert, P., and E. L. Simms. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? Evolutionary Ecology 16: 285-297.
- Andersson, J., P. Byström, D. Claessen, L. Persson, and A. M. De Roos. 2007. Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. The American Naturalist 169: 820-829.
- Bronte, C. R., M. E. Holey, C. P. Medenjian, J. L. Jonas, R. M. Claramunt, P. C. McKee, M. L. Toneys, M. P. Ebener, B. Breidert, G. W. Fleischer, R. Hess, A. W. Martell, Jr., and E. J. Olsen. 2007. Relative abundance, site fidelity, and survival of adult Lake Trout in Lake Michigan from 1999 to 2001: Implications for future restoration strategies. North American Journal of Fisheries Management 27: 137-155.
- Brown, E. J., Jr., W. G. Eck, N. R. Foster, R. M. Horrall, and C. E. Coberly. 1981. Historical evidence for discrete stocks of Lake Trout (*Salvelinus namaycush*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 38: 1747-1758.
- Burnham-Curtis, M. K., C. C. Krueger, D. R. Schreiner, J. E. Johnson, T. J. Stewart, R. M. Horrall, W. R. MacCallum, R. Kenyon, and R. E. Lange. 1995. Genetic strategies for Lake Trout rehabilitation: a synthesis. Journal of Great Lakes Research 21: 477-486.
- Chavarie, L., K. L. Howland, and W. M. Tonn. 2013. Sympatric polymorphism in Lake Trout: the coexistence of multiple shallow-water morphotypes in Great Bear Lake. Transactions of the American Fisheries Society 142: 814-823.

- Christie, W. J. 1974. Changes in the fish species of the Great Lakes. *Journal Fisheries Research Board of Canada* 31: 827-854.
- Dawson, K. A., R. L. Eshenroder, M. E. Holey, and C. Ward. 1997. Quantification of historic Lake Trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2290-2302.
- Edsall, T. A., and G. W. Kennedy. 1995. Availability of Lake Trout reproductive habitat in the Great Lakes. *Journal of Great Lake Research* 21: 290-301.
- Eschmeyer, P. H., and A. M. Phillips, Jr. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. *Transactions of the American Fisheries Society* 94:62-74.
- Eshenroder, R. L., C. R. Bronte, J. W. Peck. 1995. Comparison of Lake Trout-egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. *Journal of Great Lakes Research* 21(Supplement 1): 313-322.
- Eshenroder, R. L. 2008. Differentiation of deep-water Lake Charr *Salvelinus namaycush* in North American lakes. *Environmental Biology of Fishes* 83: 77-90.
- Fenderson, O. C. 1964. Evidence of subpopulations of lake whitefish, *Coregonus clupeaformis*, involving a dwarf form. *Transactions of the American Fisheries Society* 93: 77-94.
- Fisher, S. J., and B. L. Swanson. 1996. Diets of siscowet Lake Trout from the Apostle Islands region of Lake Superior, 1993. *Journal of Great Lakes Research* 22: 463-468.
- Franssen, N. R. 2011. Anthropogenic habitat alteration induces rapid morphological divergence in native stream fish. *Evolutionary Applications* 4: 791-804.
- Gíslason, D., M. M. Ferguson, S. Skúlason, and S. S. Snorrason. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2229–2234.

- Guinand, B., K. T. Scribner, K. S. Page, and M. K. Burnham-Curtis. 2003. Genetic variation over space and time: analyses of extinct and remnant lake trout populations in the upper Great Lakes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270: 425-433.
- Hansen, M. J. 1999. Lake Trout in the great lakes: basinwide stock collapse of binational restoration. In: Taylor, W.W., and C. P. Ferreri, editors. *Great lakes fisheries policy and management: a binational perspective*. Michigan: Michigan State University Press. p. 417-453.
- Holey, M. E., R. W. Rybicki, G. W. Eck, E. H. Brown Jr, J. E. Marsden, D. S. Lavis, M. L. Toneys, T. M. Trudeau, and R. M. Horrall. 1995. Progress toward Lake Trout restoration in Lake Michigan. *Journal of Great Lakes Research* 2 (Supplement 1):128-151.
- Janssen J., J.E. Marsden, C.R. Bronte, D.J. Jude, S.P. Sitar, F.W. Goetz. 2007. Challenges to deep-water reproduction by Lake Trout: Pertinence to restoration in Lake Michigan. *Journal of Great Lakes Research* 33 (Supplement 1): 59-74.
- Jonsson, B., and N. Jonsson. 2001. Polymorphism and speciation in Arctic charr. *Journal of Fish Biology* 21: 71-86.
- Kahilainen, K., and K. Ostbye. 2006. Morphological differentiation and resource polymorphism in three sympatric Whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *Journal of Fish Biology* 68: 63-79.
- Kirkpatrick, M., and R. K. Selander. 1979. Genetics of speciation in lake whitefishes in the Allegash basin. *Evolution* 33: 478-485.

- Kruger, C. C., and P. E. Ihssen. 1995. Review of genetics of Lake Trout in the Great Lakes: history, molecular genetics, physiology, strain comparisons, and restoration management. *Journal of Great Lakes Research* 21 (Supplement 1): 348-363.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Lindsey, C. C. 1964. Problems in zoogeography of the Lake Trout, *Salvelinus namaycush*. *Journal of the Fisheries Research Board of Canada* 21: 977-994.
- Marsden, J. E., J. M. Casselman, T. A. Edsall, R. F. Elliot, J. D. Fitzsimons, W. H. Horns, B. A. Manny, S. C. McAughey, P. G. Sly, and B. L. Swanson. 1995. Lake Trout spawning habitat in the Great Lakes a review of current knowledge. *Journal of Great Lakes Research* 21 (Supplement 1): 487-497.
- Moore, S. A., and C. R. Bronte. 2001. Delineation of sympatric morphotypes of Lake Trout in Lake Superior. *Transactions of the American Fisheries Society* 130: 1233-1240.
- Muir, A. M., P. Vecsei, and C. C. Krueger. 2012. A perspective on perspectives: methods to reduce variation in shape analysis of digital images. *Transactions of the American Fisheries Society* 141: 1-10.
- Nordeng, H. 1983. Solution to the “char problem” based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1372–1387.
- Page, K. S., K. T. Scribner, M. Burnham-Curtis. 2004. Genetic diversity of wild and hatchery Lake Trout populations: Relevance for management and restoration in the Great Lakes. *Transactions of the American Fisheries Society* 133: 674-691.

- Parsons, K. J., B. W. Robinson, and T. Hrbek. 2003. Getting into shape: An empirical comparison of traditional truss-based morphometric methods with a newer geometric method applied to new world Cichlids. *Environmental Biology of Fishes* 67: 417-431.
- Perkins, D. L., and C. C. Krueger. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at stony island reef, Lake Ontario. *Journal of Great Lakes Research* 21 (Supplement 1): 400-417.
- Pigeon, D., A. Chouinard, and L. Bernatchez. 1997. Multiple modes of speciation involved in the parallel evolution of sympatric morphotypes of lake whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* 51: 196-205.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. *The American Naturalist* 144: 596-627.
- Rohlf, J. F. 1990. Morphometrics. *Annual Review of Ecology and Systematics* 21: 299-316.
- Scott, I. D. 1921. Inland lakes of Michigan. Wynkoop, Hallenbeck, Lansing Michigan.
- Skúlason, S., and T. B. Smith. 1995. Resource polymorphism in vertebrates. *Trends in Ecology and Evolution* 10: 366-370.
- Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* 31: 111-133.
- Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience* 39: 436-445.
- Svanbäck, R., P. Eklöv, R. Fransson, and K. Holmgren. 2008. Interspecific competition drives multiple species resource polymorphism in fish communities. *Oikos* 117: 114-124.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* 20: 249-278.

- Whitman, D.W. and Agrawal, A.A. 2009. What is phenotypic plasticity and why is it important? In: Whitman, D.W. and T. N. Ananthakrishnan, editor. Phenotypic plasticity of insects: mechanisms and consequences. Science Publishers. p. 1-63.
- Wilberg, M. J., M. J. Hansen, and C. R. Bronte. 2003. Historic and modern abundance of wild lean Lake Trout in Michigan waters of Lake Superior: implications for restoration goals. North American Journal of Fisheries Management 23: 100-108.
- Wilson, C. C., and N. E. Mandrak. 2004. History and evolution of lake trout in Shield lakes: past and future challenges. Boreal Shield watersheds: lake trout ecosystems in a changing environment. Boca Raton, Florida: Lewis Publishers, CRC Press. p. 21-35.
- Wimberger, P. H. 1992. Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae). Biological Journal of the Linnean Society 45: 197-218.
- Zimmerman, M. S., C. C. Krueger, R. L. Eshenroder. 2006. Phenotypic diversity of Lake Trout in Great Slave Lake: differences in morphology, buoyancy, and habitat depth. Transactions of the American Fisheries Society 135: 1056-1067.
- Zimmerman, M., C. Krueger, and A. Muir. 2012. Draft instructions for analyzing Lake Trout and cisco body shape using the TPS software suite.
- Zimmerman, M., S., S. N. Schmidt, C. C. Krueger, M. J. Vander Zanden, and R. L. Eshenroder. 2009. Ontogenetic niche shifts and resource partitioning of Lake Trout morphotypes. Canadian Journal of Fisheries and Aquatic Sciences 66: 1007-1018.

CHAPTER II

POPULATION CHARACTERISTIC COMPARISON BETWEEN LEAN LAKE TROUT FROM ELK LAKE (ANTRIM COUNTY), MI, LAKE MICHIGAN, AND LAKE SUPERIOR

Introduction

The Lake Trout in Elk Lake exhibit unique characteristics with distinguishable characteristics in morphology, genetics, and behavioral ecology relative to other populations of Lake Trout in the Great Lakes (see Chapter 1). Understanding the inherent characteristics of a population including the growth rate (Fraley and Shepard 1989; Shuter et al. 1998) and abundance are important for making effective management decisions (Peterson et al. 2004). These characteristics are influenced by genetics (Burnham-Curtis et al. 1995; Gale et al. 2013; Johnson et al. 2001), food availability (Michalsen et al. 1998; Johnson et al. 2001; Jones 1986), temperature (Hofmann and Fischer 2003; Neverman and Wurtsbaugh 1994), metabolism (Michalsen et al. 1998), disease, and parasitism (Johnson et al. 2001).

The objectives of this study were to 1) estimate the abundance of the Lake Trout population in Elk Lake using information gathered from a field sampling creel survey, angler diary program, and angler tag returns; 2) describe differences in age and growth between the lean form of Lake Trout from Elk Lake, stocked lean form of Lake Trout from Lake Michigan, and the lean form of Lake Trout from Lake Superior.

Methods

Study Site

Sampling was conducted in Elk Lake, Antrim County, Michigan (Figure 1). Elk Lake is a small, inland lake approximately 14.4 km in length and 3.2 km wide at its widest point with a

maximum depth of 61 m and primarily clay substrate (Scott 1921). Elk Lake was once connected to Lake Michigan through Grand Traverse Bay but was hydrologically separated when a dam was installed in 1856 (Scott 1921). Elk Lake is the final lake in the chain of lakes watershed that spans Antrim, Charlevoix, Grand Traverse, and Kalkaska Counties, Michigan.

Field Sampling

Adult Lake Trout were captured in Elk Lake with trap nets (1.8 m wide x 152.4 m long with 6.4 cm mesh) in fall and spring 2009 and bottom gill nets (6 m wide x 900 m long with 7.6 cm mesh) in fall and spring of 2009, 2011, and 2012. During spring 2009, trap nets (n=13) and bottom gill nets (n=4) were set in waters depths of <7.6 m and >30.5 m, respectively. In fall 2009, bottom gill nets (n=4) were set in water depths <18.3 m, while two bottom gill nets were set at depths 18.3-40 m. During fall 2011, 69 bottom gill nets were set in the western side of Elk Lake in water depths 24.4-60 m for one hour sets to decrease the risk of mortality and by-catch. In spring 2012, 44 bottom gill nets in water depths 24.4-60 m were set primarily on the northern and western portions of the lake. During fall 2012, 75 bottom gill nets were set in depths ranging from 24.4-60 m.

For each Lake Trout captured the total length (mm) was recorded, scale samples were removed from below the dorsal fin (Murphy and Willis, 1996), and a lower caudal fin clip was collected for genetic analysis. Otoliths were removed from any individual that had died during sampling for aging. To evaluate population size we conducted mark-recapture population assessments. Individuals alive at the time of capture were held in a live well and tagged with a 17.145 cm lock tag placed near the front of the dorsal fin. Tagged fish were released near the point of capture.

Age and Growth

Lake Trout ages were determined by counting annuli on scales (live-released fish) and otoliths (dead fish). Scales were prepared by wet mounting them between slides (Hubert et al. 1987). Otoliths were prepared by sanding the otolith down to the center annuli (Barnett-Johnson et al. 2008) and burning the edge (Christensen 1964). Scale and otolith images were taken using Image Pro-Plus 5.1 and a Nikon SMZ 800 camera. Scale and otolith images were aged by two readers to determine agreement. If ages did not match among readers, a third reader provided an age estimate. Final ages were determined when ages from two agers agreed or as the average age when the three agers each deviated by one year. When there were >2 years of disagreement among the three readers, the fish were eliminated from age analysis. When available, otoliths were used to determine the final age of a fish. Fish used in growth calculations from Elk Lake and Lake Michigan were captured in 2009-2012, while fish from Lake Superior were captured in 2008. Length-at-age values for Lake Michigan Lake Trout were collected near Grand Traverse Bay, Michigan, and in southern Lake Michigan using bottom gill nets and provided by the Michigan Department of Natural Resources. Length-at-age values for Lake Superior Lake Trout were collected near Isle Royal, Michigan and provided by the Michigan Department of Natural Resources.

Given the small sample size, length-at-age estimates were back calculated for Elk Lake to increase the number of length estimates per age group. For each fish where a final age was determined, measurements were taken along a radius drawn the length of the dorsal axis, from the center of the focus to the furthest point on the outer edge of each scale. The length of each annular increment was measured from the center of the focus to the outer edge of each annulus. The distance between the focus and each annulus was used to back-calculate individual Lake

Trout total length at every age. The growth rate for the Elk Lake Lake Trout was estimated using the Fraser-Lee method of back-calculation in FishBC 2.0, scale measurements were taken in FishBC 3.10, and the total length of each individual Lake Trout (Carlander 1982; Frie 1982).

The formula used for back-calculation was:

$$L_i = \frac{L_c - a}{S_c} S_i + a$$

where L_i represents the back-calculated length of the fish when the i th increment was formed, L_c represents the length of the fish at capture, S_c represents the radius of the hard part at capture, S_i is the radius of the hard part at the i th increment, and a is the y-intercept (Murphy and Willis 1996).

Von Bertalanffy growth models were used to evaluate growth patterns for lake trout in Elk Lake and Lake Michigan. The formula used for the von Bertalanffy growth model was:

$$L_t = L_{\infty,4-11} (1 - e^{-K_{4-11}(t-t_0)}) + \varepsilon$$

where L_{∞} is the asymptotic length (mm) for fish ages 4 to 11, K is the growth coefficient for fish ages 4 to 11, t_0 is the hypothetical age when the fish length is equal to zero, and L_t is the length at age t (Johnson et al. 2001). Von- Bertalanffy models were calculated from mean length-at-age data for each population. Only fully represented age groups ages 4 to 11 were used in the estimation process, and the y-intercept was set to zero.

Angler Harvest

A creel survey and angler diary program was used during the summer of 2012 to gather additional population data and determine if angling impacts the Elk Lake Lake Trout population during the summer. The creel survey occurred June and July of 2012; four week days and four weekend days were randomly sampled each month. During each month, two weekdays and two

weekend days were randomly assigned as shift A (June and July 600-1430), while the other two weekdays were randomly assigned as shift B (June: 1330-2200; July: 1430-2300). A count of the number of boats on Elk Lake occurred once every shift at random times from eight lookout points around Elk Lake. Every angler encountered was interviewed about their background and their fishing trip (Appendix A).

An angler diary program was initiated in July 2012 and continued through the 2013 ice fishery. The survey was designed to determine if angling impacted the Elk Lake Lake Trout population and to gather additional population data on Lake Trout. Participants were located through word of mouth and advertisement through the Elk-Skegemog Lakes Association. Each angler was given a journal and asked to record information about fishing trips throughout the season, including details of their catch (Appendix B). Anglers returned their diaries at the end of the season, and another diary was sent to them to continue the program when requested. Anglers not participating in the angler diary program were encouraged through advertisements and word of mouth to report the capture of any tagged Lake Trout from Elk Lake.

Population Estimate

Population abundance was calculated using the Petersen method with the Chapman modification because sampling during the recapture period was done without replacement (Chapman 1951; Van Den Avyle and Hayward 1999). The formula used was:

$$N = \frac{(M+1)(C+1)}{(R+1)} - 1$$

where N is the population abundance, M is the number of fish initially marked and released, C is the number of fish collected and examined for tags in the second period, and R is the number of recaptures during the second period (Van Den Avyle and Hayward 1999). The number of fish

tagged during the 2011-2013 sampling periods were pooled together and used to calculate the value for M , the total of marked and unmarked fish caught by anglers during 2011-2013 was used to determine the value for C , and the number of tag returns reported by anglers was used for R . The variance was calculated using the formula:

$$V(N) = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}$$

where N is the population abundance, M is the number of fish initially marked and released, C is the number of fish collected and examined for tags in the second period, and R is the number of recaptures during the second period (Van Den Avyle and Hayward 1999).

Results

Field Sampling

During spring 2009, trap nets captured one Lake Trout while bottom gill nets captured three Lake Trout in one of the deep nets and no Lake Trout in the shallower nets. In fall 2009, bottom gill nets set in <18.3 m of water captured no Lake Trout, while nets in 18.3-40 m captured three and 12 Lake Trout, respectively. During fall 2011, 184 Lake Trout were collected, and 142 Lake Trout were tagged and released. In spring 2012, 40 Lake Trout were caught; 31 Lake Trout were tagged and released. In fall 2012, 78 Lake Trout were captured; 60 Lake Trout were tagged and released.

Age and Growth

Most individuals captured between 2009-2012 were between 4-6 years old, while the majority of fish captured were 5 years old (Figure 9). The first two readers were in agreement for 32% of the structures aged. The remaining 68% of structures were given to a third reader.

Of the final ages assigned, 6% deviated between the first two readers by one year, and the midpoints between the ages were assigned. Eleven percent were structures where reader ages deviated by >2 years; these were eliminated from further analysis. Lake Michigan Lake Trout had higher mean length-at-age values for all ages than Lake Trout from Elk Lake and Lake Trout from Lake Superior (Figure 10). For ages 4-11, Lake Michigan Lake Trout also had a greater asymptotic average maximum body size ($L_{\infty, \text{age } 4-11}=779$ mm) than the Elk Lake population ($L_{\infty, \text{age } 4-11}=669$ mm) and the Lake Superior population ($L_{\infty, \text{age } 4-11}=620$ mm), while the Elk Lake population had a larger growth rate coefficient ($k_{\text{age } 4-11}=0.35$) than Lake Michigan population ($k_{\text{age } 4-11}=0.24$), and the Lake Superior population ($k_{\text{age } 4-11}=0.18$; Figure 11). Younger individuals (ages 4 and 5) in Elk Lake grew faster than the Lake Michigan and Lake Superior populations at a comparable age. At approximately age 5, the Elk Lake growth rate plateaued, resulting in slowed growth for fish >5 years of age. In contrast, Lake Michigan fish >5 years of age appear to be growing faster and reaching a larger mean asymptotic length than lake trout from Elk Lake and Lake Superior (Figure 11).

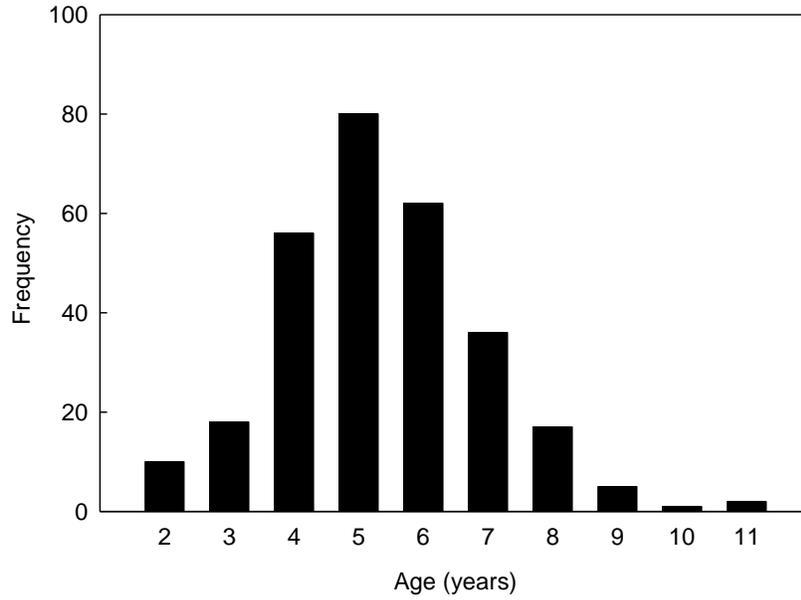


Figure 9. Age frequencies of Lake Trout from Elk Lake, Michigan, sampled during the 2009-2012 sampling seasons.

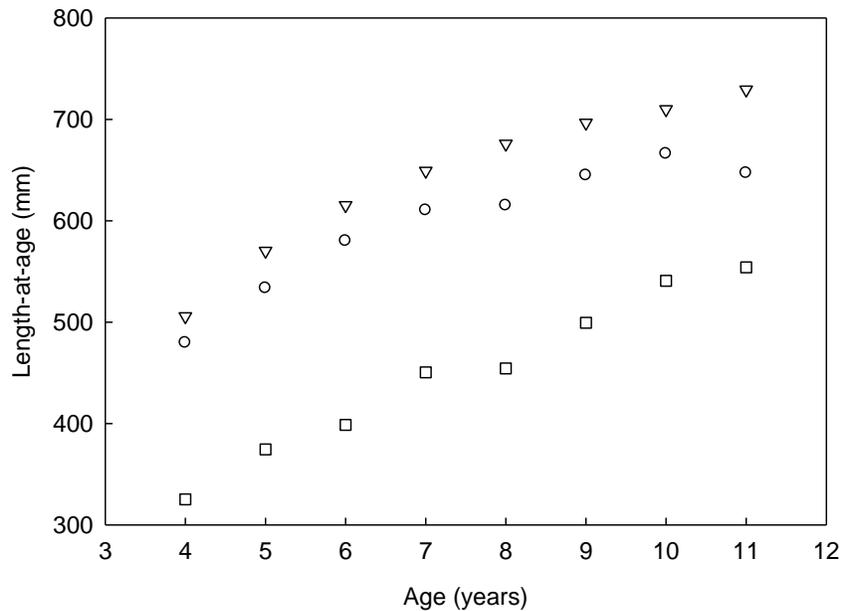


Figure 10. Mean length-at-age (mm) of Lake Trout from Elk Lake, Michigan (back-calculated; circles), Lake Michigan (measured; triangles), and Lake Superior (measured; squares) for ages 4-11.

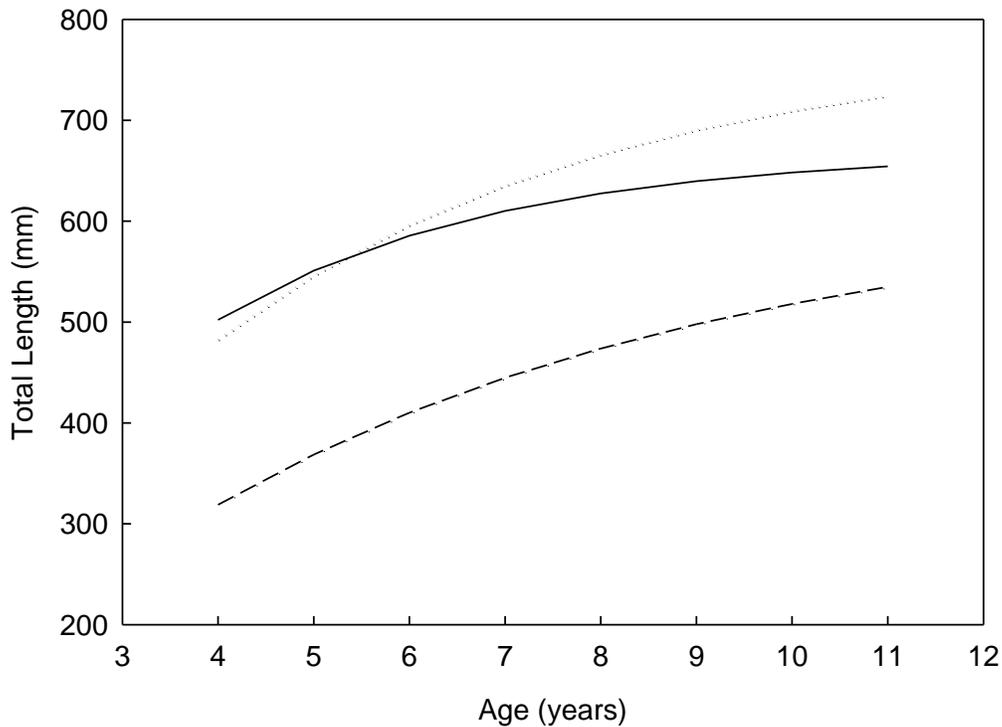


Figure 11. Von Bertalanffy model estimates for Lake Trout from Elk Lake, Michigan (solid line), Lake Michigan (dotted line), and Lake Superior (dashed line) for ages 4-11. Models were estimated from back-calculated lengths in Elk Lake and observed values from Lake Michigan and Lake Superior.

Harvest Estimates

During the month of June and July 2012, 24 fishing boats and 125 non-fishing boats were observed during the count of the number of boats on Elk Lake that occurred during each creel shift, while 10 anglers were observed fishing from the shore or dock. A total of 25 interviews were taken during the month of June and July 2012, comprised mostly of anglers fishing from a boat. In total, 450 fish were recorded as catch during the summer of 2012. Yellow Perch (*Perca flavescens*) comprised the majority of the total catch, followed by Smallmouth Bass (*Micropterus dolomieu*), Rock Bass (*Ambloplites rupestris*), Muskellunge (*Esox masquinongy*),

and Rainbow Trout (*Oncorhynchus mykiss*). In both June and July, two anglers interviewed targeted Lake Trout, but no Lake Trout were captured or recaptured.

Catch information from the angler diary program and individual angler reports resulted in the only recaptures of tagged Lake Trout throughout the study. Eighty-five unmarked Lake Trout and 36 tagged Lake Trout were captured and reported by anglers. Thirty of the unmarked Lake Trout were captured during the summer months of May, June, July, and August, while the remaining 55 were captured during September, October, November, February, March, and April, indicating the winter ice fishery is more active for Lake Trout fishing than fisheries in the summer months.

Population Estimate

The population of Lake Trout in Elk Lake was estimated at 1,001 fish ($\sigma^2 = 16,748$; 95% CI=749-1255 fish) for ages 2 to 11.

Discussion

Growth patterns differed among the Lake Trout from Elk Lake, Lake Michigan, and Lake Superior. Lake Trout greater than age 5 from Elk Lake had substantially slower growth rates than observed for Lake Trout from Lake Michigan. The Lake Superior population was slower growing than both Lake Michigan and Elk Lake for all age groups. Genetic differences can have an impact on growth rates between different fish strains (Silverstein et al 1999; Valente et al. 1999), and the genetic differences between the Lake Trout from Elk Lake, Lake Michigan, and Lake Superior (Michigan State University; Dr. Kim Scribner, unpublished data) may be responsible for the different growth rates. Resource availability and diet can also influence life history traits (Jonsson et al. 1999), and growth rates can be affected by prey size (Madenjian et

al. 1998; Wankowski and Thorpe 1979) and prey type, with faster growth observed in piscivorous fish (Jonsson et al. 1999). If the need for larger prey is not met as a fish grows, growth may slow or cease all together (Jonsson et al. 1999; Mittelbach 1983). Through preliminary stomach analyses, Lake Trout in Elk Lake eat primarily fish during the fall and macroinvertebrates during the spring (Michigan Department of Natural Resources; Jory Jonas, unpublished data). Prey limitations may be responsible for the slow growth observed in the Elk Lake Lake Trout after age 5, but additional diet and behavioral analyses are needed to draw further conclusions.

The winter ice fishery is the most active season for Lake Trout angling. The tendency of anglers to remove the largest individuals from a population can influence evolutionary change (Law 2000) and impact growth rates (Biro and Post 2008). Minimum size limits for Lake Trout in Elk Lake are larger (38.1 cm) than in Lake Michigan (28.4 cm). Over time, this size selective angling during the Elk Lake winter ice fishery removes large and late maturing individuals, while leaving behind slow growing and early maturing fish (Biro and Post 2008; Law 2000).

The Petersen method estimated a fairly small population of Lake Trout in Elk Lake with a large variance. To further increase the number of tag returns for the population estimate, future research should survey the winter ice fishery and continue the angler diary program, as many assumptions were violated while sampling (Van Den Avyle and Hayward 1999). The Petersen method can overestimate population size by underrepresenting marked fish in the recapture period, and not all anglers who captured a tagged fish likely reported resulting in an overestimate of the population abundance.

The Elk Lake Lake Trout display different life history characteristics relative to other forms of Lake Trout in the Great Lakes Their distinct behavior and growth patterns demonstrate

that this is a unique population. Further research should continue to elucidate additional defining features and determine if they are a viable source to re-introducing lost diversity via stocking in the Great Lakes.

LITERATURE CITED

- Barnett-Johnson, R., T. E. Pearson, F. C. Ramos, C. B. Grimes, and R. B MacFarlane. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape ecology. *Limnology and Oceanography* 53: 1633-1642.
- Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America* 105: 2919-2922.
- Burnham-Curtis, M. K., C. C. Krueger, D. R. Schreiner, J. E. Johnson, T. J. Stewart, R. M. Horrall, W. R. MacCallum, R. Kenyon, and R. E. Lange. 1995. Genetic strategies for Lake Trout rehabilitation: a synthesis. *Journal of Great Lakes Research* 21: 477-486.
- Carlander, K.D. 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. *T. Am. Fish Soc.* 111, 332-336.
- Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. *University of California Publications in Statistics* 1: 131-160.
- Christensen, J. M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. *ICES Journal of Marine Science* 29: 73-81.
- Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and river system, Montana. *Northwest Science* 63: 133-143.
- Frie, R.V. 1982. Measurement of fish scales and back-calculation of body-lengths using a digitizing pad and microcomputer. *Fisheries*: 7: 5-8.

- Gale, B. H., J. B. Johnson, G. B. Schaalje, and M. C. Belk. 2013. Effects of predation environment and food availability on somatic growth in the livebearing fish *Brachyrhaphis rhabdophora* (Pisces: Poeciliidae). *Ecology and Evolution* 3: 326-333.
- Hofmann, N., and P. Fischer. 2003. Impact of temperature on food intake and growth in juvenile burbot. *Journal of Fish Biology* 63: 1295-1305.
- Hubert, W. A., G.T. Baxter, and M. Harrington. 1987. Comparison of age determinations based on scales, otoliths and fin rays for cutthroat trout from Yellowstone Lake. *Northwest Science* 61: 32-36.
- Johnson, T. B., L. Hartt, and D. M. Mason. 2001. Constraints to growth of Lake Superior Lake Trout, *Salvelinus namaycush*. Great Lakes Fishery Commission Project Completion Report.
- Jones, G. P. 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70: 136-139.
- Jonsson, N., T. F. NÆsje, B. Jonsson, R. SaksgÅrd and O. T. Sandlund. 1999. The influence of piscivory on life history traits of brown trout. *Journal of Fish Biology* 55: 1129-1141.
- Law, R. 2000. Fishing, Selection, and phenotypic evolution. *ICES Journal of Marine Science* 57: 659-668.
- Madenjian, C. P., T. J. DeSourcie, and R. M. Stedman. 1998. Ontogenic and spatial patterns in diet and growth of Lake Trout in Lake Michigan. *Transactions of the American Fisheries Society* 127: 236-252.
- Michalsen, K., G. Ottersen, and O. Nakken. 1998. Growth of North-east arctic cod (*Gadus morhua* L.) in relation to ambient temperatures. *ICES Journal of Marine Science* 55: 863-877.
- Mittelbach, G. G. 1983. Optimal foraging and growth in bluegills. *Oecologia* 59: 157-162.

- Murphy, B. R., and D. W. Willis, editors. 1996. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration of juvenile fish, *Cottus extensus*. *Oecologia* 98: 247-256.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of Brook Trout on native Cutthroat Trout. *Ecological Applications* 14: 754-772.
- Shuter, B. J., M. L. Jones, R. M. Korver, N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: the inland Lake Trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2161-2177.
- Silverstein, J. T., W. R. Wolters, and M. Holland. 1999. Evidence of differences in growth and food intake regulation in different genetic strains of channel catfish. *Journal of Fish Biology* 54: 607-615.
- Wankowski, J. W. J., and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar L.*). *Journal of Fish Biology* 14: 351-370.
- Van Den Avyle, M.J., Hayward, R.S. 1999. Dynamics of exploited fish populations in Kohler, C.C., Hubert, W.A., (eds.), *Inland Fisheries Management in North America*. American Fisheries Society, Bethesda, Maryland, pp 127-166.
- Valente, L. M. P., E. Rocha, E.F.S. Gomes, M. W. Silva, M. H. Oliveira, R. A. F. Monteiro, and B. Fauonneau. 1999. Growth dynamics of white and red muscle fibres in fast- and slow-growing strains of rainbow trout. *Journal of Fish Biology* 55: 675-691.

APPENDICES

APPENDIX A

QUESTIONS ANGLERS WERE ASKED DURING THE SUMMER 2012 CREEL SURVEY ON ELK LAKE, MICHIGAN.

Data collected by clerk before angler is approached for an interview	Data collected by clerk during the interview
Site name	Number of lines fished
Mode of angler fishing (e.g. from boat, shore, pier, ect.)	Number of trips the angler has made that day total
Number of anglers	Number of days fished at this site over the past three months
	Complete or incomplete interview
	Primary method angler is using to fish
	Primary bait angler is using to fish
	Species angler is targeting
	Angler's age (optional)
	Angler's zip code (optional)
	Angler's sex (optional)
	Date/time angler began fishing
	date/time angler stopped fishing
	Number and type of all species harvested
	Number and type of all species released

APPENDIX B
 INFORMATION COLLECTED FROM THE ANGLER DIARIES GIVEN TO EACH
 PARTICIPANT IN THE ELK LAKE ANGLER DIARY PROGRAM.

General Information	Description of Catch	Lake Trout Details for each individual captured
Date	Species and number harvested	Length
Start time/end time	Species and number released	Maturity
Number of anglers		Sex
Number of lines		Tag number
Fishing mode (shore/ice/boat)		Released (yes/no)
Fishing Method (troll/still/cast/jig/drift/fly)		Additional comments
Target Species		