

Can Ratios of Linear Morphometric Measurements Delineate among Lake Trout Morphotypes?

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Abstract

Several morphotypes of Lake Trout (*Salvelinus namaycush*) were historically found in all of the Laurentian Great Lakes. However, abundance and morphological diversity were lost due to overfishing and predation by Sea Lamprey (*Petromyzon marinus*). Despite this, at least four morphotypes of Lake Trout – Lean, Siscowet, Humper, and Redfin– still exist around Isle Royale, Lake Superior. The body fat content, growth, external morphology, and genetic structure of the Lean, Humper, and Siscowet morphotypes have been described extensively. Muir *et al.* (2014) recently used a combination of morphological, ecological, and physiological characteristics to quantitatively distinguish between these three morphotypes and the Redfin, which they described. The objective of my study is to determine if simple ratios of linear morphological measurements can be used to differentiate between the four Lake Trout morphotypes. A total of 484 Lake Trout were collected in bottom-set gillnets from known spawning locations near Isle Royale in Fall 2010, 2011, and 2014. Each Lake Trout was identified as best as possible to morphotype, measured for total length, and digitally photographed with a ruler. In the laboratory, several linear measurements of the fish (e.g., head length, caudal peduncle depth) were taken from the digitized photos of the fish. Seven ratios that would be unaffected by head or total length (e.g., orbital length to head length) and were thought to discriminate between the morphotypes were constructed from the linear measurements. A multivariate linear discriminant function analysis and several clustering techniques were used to determine if statistical groupings based on our ratios matched the field identification of morphotypes. Unfortunately, discrimination among morphotypes was poor. Kmeans clustering identified three distinct clusters based on the ratio of the depth to the length of the caudal peduncle, but these clusters did not match the field identifications of morphotype. High variation in the ratios within and low variation in the ratios among morphotypes likely contributed to the inability to differentiate morphotypes. Additionally, as field identification is difficult, the field assigned morphotypes may have been incorrectly assumed to be correct. In summary, simple ratios of linear measurements alone were not enough to significantly distinguish or separate between the Lake Trout morphotypes. For future work, including ecological or physiological characteristics (e.g., capture depth, habitat type) in the models, such as in Muir *et al.* (2014), may help better discriminate among the morphotypes.

Introduction

Historically, the Laurentian Great Lakes held multiple and diverse morphotypes of Lake Trout (*Salvelinus namaycush*) (Rakestraw 1968) that were described as being easy to visually distinguish and identify (Goodier 1981). During the past century, Great Lakes food webs and especially Lake Trout have been greatly impacted by ecological and anthropogenic changes. Most of the historic Lake Trout diversity was lost due to Sea Lamprey (*Petromyzon marinus*) predation and overfishing that peaked in the 1960's (Krueger and Ihssen 1995). After Lake Trout populations crashed, plans were implemented to re-establish them in the Great Lakes. Millions of Lake Trout have been raised in hatcheries and stocked into the Great Lakes every year in this effort to re-establish Lake Trout. Sea Lamprey control has also been a large part of Lake Trout recovery, with many methods implemented to reduce the abundance of the invasive Sea Lamprey and minimize their impact on Lake Trout (Muir *et al.* 2012a). Another method of trying to re-establish Lake Trout has been creating refuges (e.g., Gull Island Shoal Refuge created in 1976) where fishing is prohibited and remaining fish populations can recover without fishing mortality (Muir *et al.* 2012a). In 1996, Lake Superior fishery agencies celebrated the recovery of Lake Trout (although not to historic numbers) and most stocking was ceased (Muir *et al.* 2012a).

Three main morphotypes of Lake Trout have been historically described -- Lean Lake Trout typically occupy shallow waters <70 m deep, Humper Lake Trout occupy offshore, midwater shoals, and Siscowet Lake Trout live in waters >100 m deep (Moore and Bronte 2001). Recently, Muir *et al.* (2014) described Redfin Lake Trout from around Isle Royale that also inhabit moderate depths (~80 m). The three historically known morphotypes (Lean, Humper, Siscowet) have been distinguished in many different ways, including by body fat content, growth, external morphology, osteology, spawning condition and timing, and genetic structure.

Eschmeyer and Phillips (1965) found that the average rate of increase in percentage fat was far greater for Siscowets than it was for Lean Lake Trout at lengths between 12 and 20 inches. Additionally, the percentage fat in the two forms was widely different and without overlap at all comparable lengths, despite substantial individual variation. Flesh samples from hatchery-reared Lean, Humper, and Siscowets, showed that the wide difference in fat content between Siscowets and Lean Lake Trout was genetically determined.

Moore and Bronte (2001) used a whole body morphometric analysis (truss protocol) to determine whether there were differences in body shape among the three main morphotypes. They found that the truss analysis could better discriminate among morphotypes than traditional morphometric characters and measurements. Principal components analysis revealed some separation (but with considerable overlap) of all three morphotypes based on head and caudal peduncle shape. Specifically, two head, three midbody, and four caudal peduncle measures

were used to correctly classify 83% of Lean, 83% of Humpers, and 80% of Siscowet Lake Trout.

Lean and Humpers Lake Trout have also been differentiated by age distributions and growth patterns. Burnham-Curtis and Bronte (1996) showed that Humpers in Lake Superior grew more slowly and matured at a smaller size than Lean Lake Trout, but the age composition of Humpers was more diverse than previously thought. In Lake Mistassini, Quebec, the Lean and Humpers Lake Trout morphotypes also differed in age, growth, and maturity, which is consistent with the resource polymorphism observed in Lake Superior (Hansen *et al.* 2012).

Spawning condition and timing may be used to distinguish between the morphotypes as well. Eschmeyer (1995) found that spawning for Leans occurred mostly from October to early November, while spawning for Siscowets occurred from June to November.

The morphotypes are also genetically distinct. Goetz *et al.* (2010) used liver transcriptomics and RNA-sequencing to identify differently expressed genes that controlled characters such as morphometry and lipid levels between morphotypes raised in identical laboratory conditions. Guinand *et al.* (2012) found significant levels of genetic differentiation among morphotypes prior to the declines in abundance due to fishing and Sea Lamprey predation. Significant levels of genetic differentiation remain among contemporary populations, though Siscowet and Lean Lake Trout lost some genetic diversity during the period of intensive fishing and Sea Lamprey predation. Thus, the period of population decline did not result in a significant loss of genetic distinctiveness among the three different morphs.

Some researchers combined several of the methods described above to differentiate between the Lake Trout morphotypes in Great Slave Lake. For example, Zimmerman *et al.* (2006) found that Lake Trout caught in less than 50 m of water were light colored, buoyantly light, and had short pectoral fins, whereas Lake Trout caught in more than 50 m were dark colored, buoyantly heavy, and had long pectoral fins. Without assigning descriptions to individuals before their analyses, they identified two phenotypic groups that corresponded to the Lean and Siscowet Lake Trout morphotypes in Lake Superior.

Understanding the patterns of Lake Trout diversity in Lake Superior will further the ongoing efforts to re-establish all forms of Lake Trout in areas where Lake Trout that have been all or mostly extirpated (Muir *et al.* 2012a). Identification of morphotypes is critical for the assessment and management of the Great Lakes Lake Trout fishery, especially if exploitation rates differ among the morphotypes (Muir *et al.* 2014). For example, Siscowet abundance has increased in Lake Superior in the last decade (Bronte *et al.* 2003), which could lead to an increase in harvest of Siscowets that could alter the composition of Lake Trout diversity. Finally, an examination of the remnant populations of Lake Trout in Lake Superior may provide insights into the ecological consequences of a century of food web and fish community alteration in the Great Lakes (Muir *et al.* 2014).

Lake Trout have been an important component of the fish community surrounding Isle Royale National Park, Lake Superior for decades (Muir *et al.* 2014). Prior to the establishment of Isle Royale National Park in 1931, the island was a popular location for the commercial fishing of Lake Trout and Lake Whitefish

(*Coregonus clupeaformis*), recreation, and as the home for several small cabins and resorts. Following the creation of the park, commercial fishing declined and ultimately ceased by the 1960's due to drastic population declines of Lake Trout (Muir *et al.* 2012a). Recreational fishing became more popular around Isle Royale after commercial fishing was stopped and Lake Trout populations began to recover. An Isle Royale strain broodstock was created to aid with the restoration efforts in Lake Superior and the other Great Lakes. It is likely that Isle Royale populations of Lake Trout were instrumental in lakewide recovery in Lake Superior.

Lean, Humper, and Siscowet Lake Trout all persist around Isle Royale (Moore and Bronte 2001). Additionally, Muir *et al.* (2014) recently quantitatively described the Redfin from waters around Isle Royale. Muir *et al.* (2014) used new methods for assessing phenotypic and ecological variation among Lake Trout around Isle Royale. They found that the four morphotypes differed in shape, buoyancy, habitat use, and traits linked to feeding and locomotion. They also found that high variation within and low variation among morphotypes led to moderately low percent agreement among visual identifications and high uncertainty in model groupings of individuals into morphotypes. They were unsure as to why there was a low level of differentiation between morphotypes but it could be due to ecological release without subsequent reorganization.

My research objective is to determine if simple ratios of linear morphological measurements can be used to differentiate between the four Lake Trout morphotypes. Ratios of simple linear measurements would be desirable for differentiating among the morphotypes because these same simple measurements could be taken in the field and the ratios calculated to aid field identification of the morphotypes. Isle Royale was chosen for the study site because its offshore location, national park status, and small, nearshore fishery makes it less disturbed than mainland areas. Therefore, it is expected to have retained more diversity in morphotypes in the surrounding waters than along the mainland shorelines.

Methods

A total of 484 Lake Trout were sampled at Isle Royale during fall spawning surveys in October 2010, October 2011, and September 2014. Previously documented spawning sites (Goodyear *et al.* 1982) and additional sites selected using more recent assessment data or data acquired from bathymetric surveys were sampled. Samples were identified by specific location using GPS and sample sites were classified by depth and habitat using LiDAR bathymetry and topography data (Wozencraft and Millar 2005). One 121.92 meter long and 1.8 meter tall graded mesh gillnet with 30.48 meter sections of 3, 4, 4.5, and 5 inches (stretch measurement) were used at each location. Nets were set on the bottom, so all fish caught were assumed to be associated with that reef at the time.

A digital image of the left side of each individual fish was taken in the field as described in Muir *et al.* (2012b). Fish with ripe gametes were considered to be spawning at that site. Capture date, depth of capture, state of maturity, fecundity (number of eggs), sex, length, and weight were collected for each fish. Also, the methods of Zimmerman *et al.* (2006) were used to measure and describe differences

in fat content and buoyancy. Understandings from previous studies were used (Moore and Bronte 2001; Bronte and Moore 2007; Zimmerman *et al.* 2006) to make an initial assessment of morphotype.

In the laboratory, digital photographs were prepared in Microsoft PowerPoint for further analysis by overlaying a grid on the fish. A five-centimeter reference bar was created if the ruler was cropped from the photo. The prepared photos were saved into Thin Plate Spline suite (TPS version 2.17, Rohlf 2013), software that allows morphometric data to be better plotted and statistically analyzed between specimen by using the transformation grid and placing landmarks according to it. In TPS, nine linear phenotypic characteristics were measured on each specimen as shown in Figure 1.

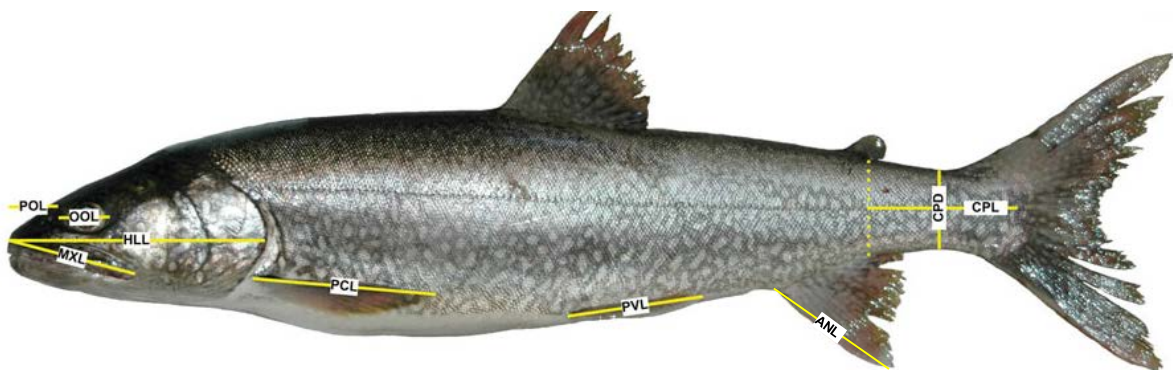


Figure 1. Nine linear phenotypic characteristics were measured on each specimen as follows – CPD: depth of the caudal peduncle at midpoint; CPL: distance along the horizontal axis of the body between the posterior of the anal fin and the caudal flexure; HLL: distance from the tip of the premaxilla to the posterior margin of the opercle; MXL: distance from the anterior point of premaxilla to posterior end of the maxilla; OOL: distance between anterior and posterior fleshy margins of the orbit; PCL: distance from the insertion of outermost ray to farthest tip of the pectoral fin; PVL: distance from the insertion of outermost ray to farthest tip of the pelvic fin; ANL: distance from the insertion of the forward most ray to the farthest tip of the anal fin; and POL: tip of the premaxilla to the anterior fleshy margin of the orbit.

The following simple ratios were created from the linear measurements to remove any length-related influence -- preorbital length (POL) divided by head length (HLL), orbital length (OOL) divided by the head length (HLL), maxilla length (MXL) divided by the head length (HLL), head length (HLL) divided by total length (TL), pectoral fin length (PCL) divided by total length (TL), anal fin length (ANL) divided by total length (TL), and caudal peduncle depth (CPD) divided by caudal peduncle length (CPL). The pelvic fin length (PVL) was not used in any ratios, as it was felt that the paired fins would be similarly affected by morphotype. Fish of both sexes were pooled for all analyses because decades of research has shown that Lake Trout are not sexually dimorphic morphologically (Esteve *et al.* 2008).

Preliminary univariate and bivariate exploratory data analyses were used to identify any possible simple measures that may differentiate among the morphotypes (as identified in the field). Specifically, one-way analysis of variance (ANOVA) models were used for each ratio to determine if the mean of the ratio differed among the four morphotypes. Scatterplots were used to determine if the morphotypes could be visually separated based on two of the ratios.

Multivariate data analysis methods were used in two different ways. First, a linear discriminant function analysis (DFA) was used to determine if linear combinations of the simple ratios could be used to correctly identify the field-identified morphotypes. A confusion matrix of the predicted morphotypes from the linear DFA and the observed field-identified morphotypes was used to assess the efficacy of the linear DFA for differentiating among the morphotypes. The linear DFA was completed with `lda()` from the MASS package (Venables and Ripley 2002) in R version 3.2.3 (R Core Team 2015). Second, two cluster methods were used with the simple ratios to identify possible clusters of similar individuals. The first cluster method used was MCluster, which does not require any prior knowledge of the number of clusters to identify, but rather uses the Bayesian Information Criterion (BIC) to identify which model (number of clusters) is most highly supported by the data (Muir et al. 2014). The MCluster cluster analysis was performed with `Mclust()` from the `mclust` package (Fraley *et al.* 2012) in R. The second clustering method was the Kmeans cluster analysis. The number of clusters suggested by Mclust was used as the required number of groups for the Kmeans clustering. Kmeans clustered the individuals based on the first two linear principal components (PC) and determined the variability that was explained by the analysis as well as the amount of separation between clusters. Clusters returned by both methods were compared against the field-identified morphotypes to determine if any cluster corresponded to any morphotype. In addition, the variables that contributed the most to each coordinate (PC) in the analysis were analyzed to determine which variables provided the most separation among clusters (not necessarily morphotypes).

Results

Exploratory univariate data analysis showed some promise for separating among the morphotypes. The preorbital/head, orbital/head, and maxilla/head ratios discriminated between the most morphotypes at one time. Lean Lake Trout had the largest mean preorbital/head ratio, Humpers had the smallest, and Redfin and Siscowet were between and were statistically similar (Figure 2). Humpers had the largest mean orbital/head ratio, Redfin and Siscowet were between and statistically similar, and Leans were the smallest (Figure 3). Lean and Redfin morphotypes were statistically similar and had the largest mean maxilla/head ratio, Siscowets were in the middle, and Humpers had the smallest (Figure 4).

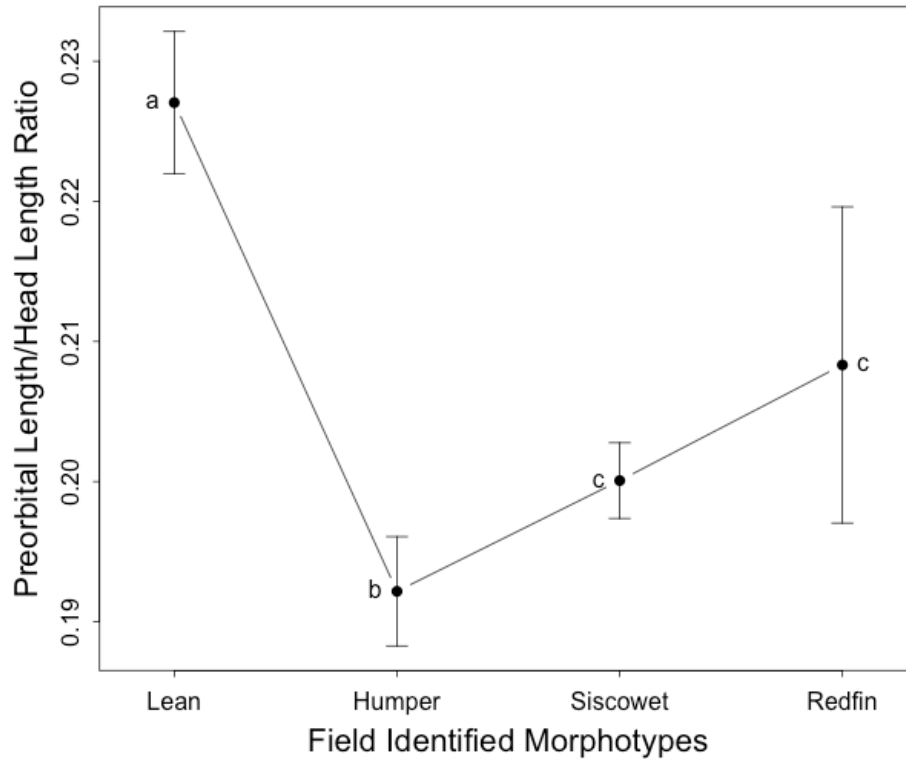


Figure 2. Mean preorbital/head ratios by morphotype with 95% confidence intervals. Means with a common letter are not statistically different.

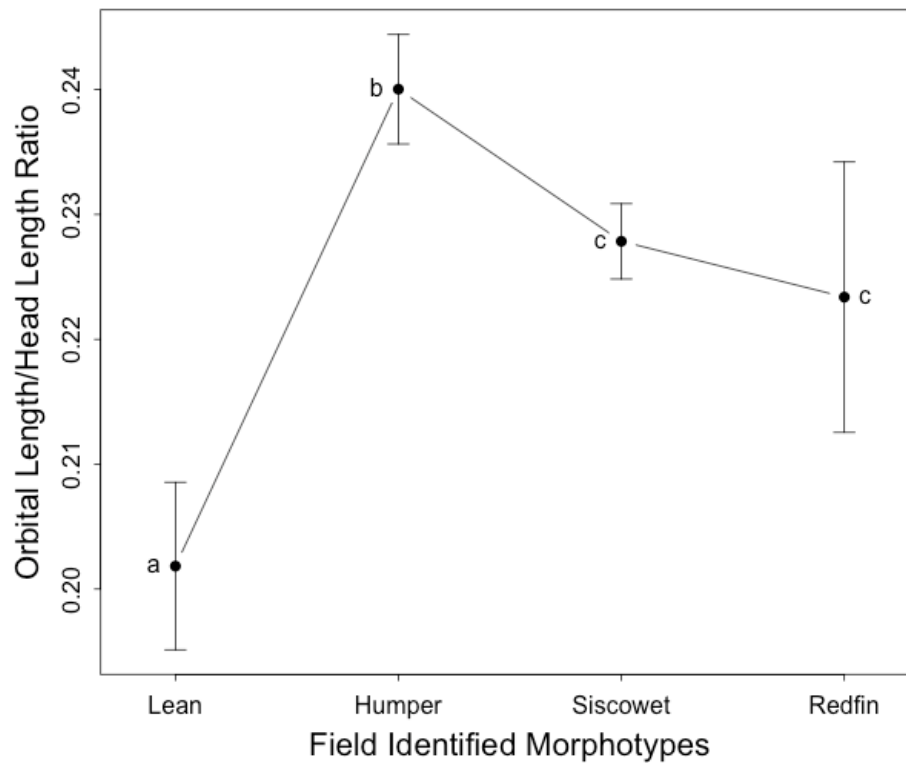


Figure 3. Mean orbital/head ratios by morphotype with 95% confidence intervals. Means with a common letter are not statistically different.

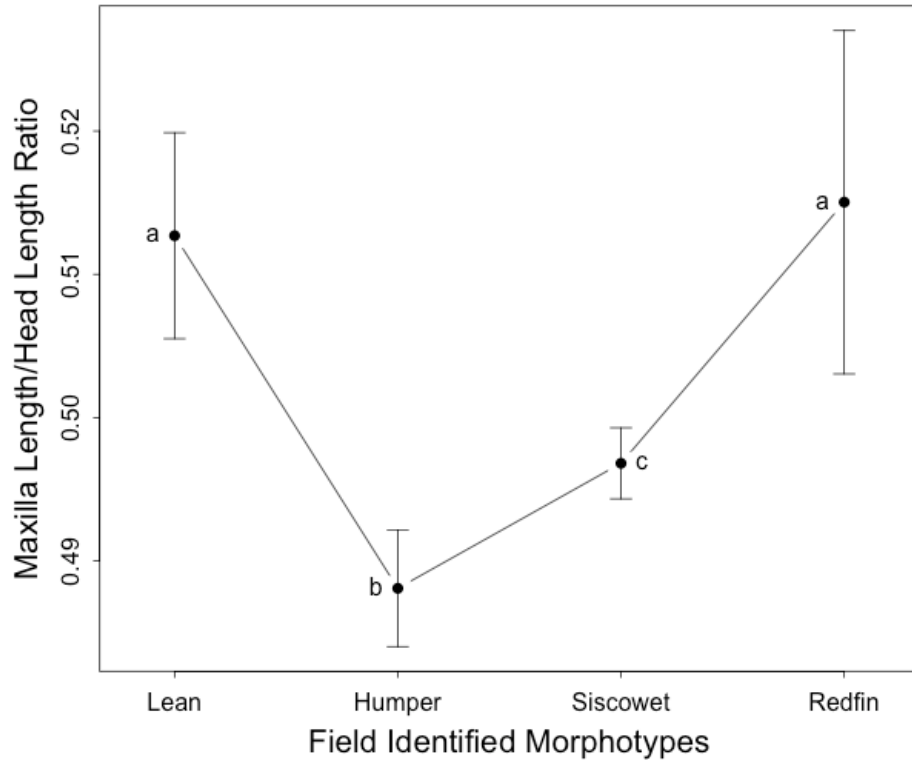


Figure 4. Mean maxilla/head ratios by morphotype with 95% confidence intervals. Means with a common letter are not statistically different.

Exploratory bivariate analysis found that although there seemed to be some separation, it didn't look as promising as the univariate analyses (Figure 5). As an example, the best apparent separation was for the preorbital to head ratio against the orbital to head ratio (Figure 5). In this plot there seems to be some separation between Lean and Humper Lake Trout, but Siscowet and Redfin Lake Trout were quite variable and extensively overlapped the Lean and Humper Lake Trout.

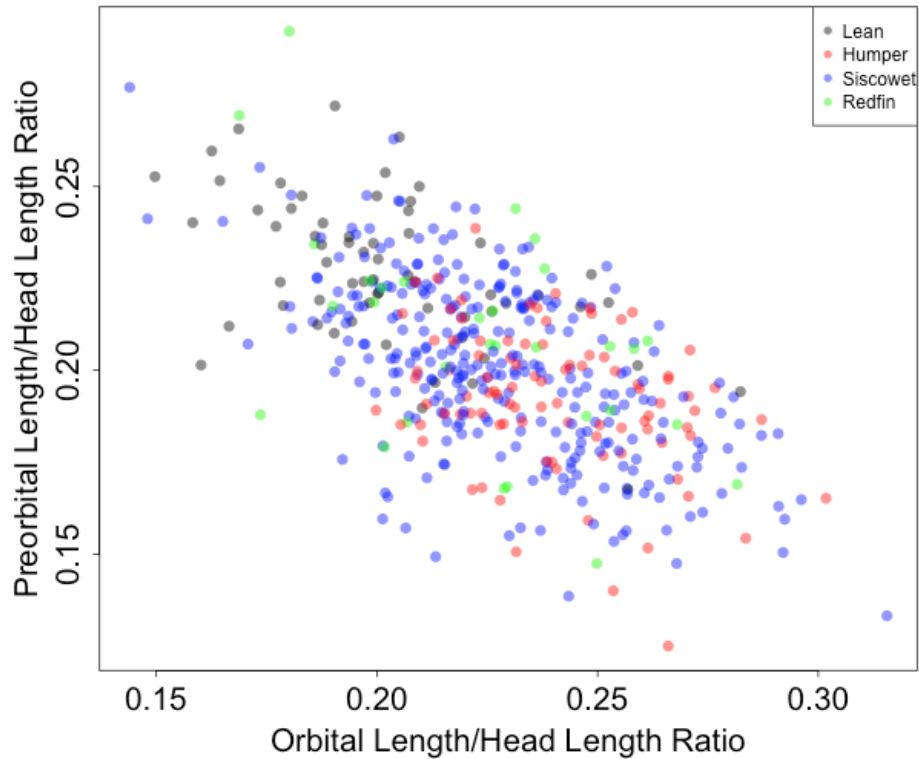


Figure 5. Scatterplot of orbital/head against preorbital/head ratio with each morphotype represented as a different color.

The groups defined by the linear DFA matched the field-identified morphotypes for 63.2% of the fish (Table 1). Siscowets were most often correctly matched (92.6%), but other morphotypes were often misclassified as Siscowet (Table 1). Humper (5.3%) and Redfin (16.7%) had the lowest correct matches, whereas Leans (32.3%) were correctly classified for about one third of the individuals.

Table 1. Confusion table that shows the frequency of individuals by Linear DFA ratio groups and field-identified morphotypes.

Field ID	Linear DFA Ratio Groups			
	Lean	Humper	Siscowet	Redfin
Lean	20	0	40	2
Humper	0	5	87	2
Siscowet	13	6	276	3
Redfin	1	0	24	5

Mclust clustering analysis found that three groups paired with model VEE had the highest BIC, indicating that it had the highest support (Figure 6). The BIC was quite similar for many other models and number of groups, which indicates that the groups and models differ little and overall separation is poor. Three groups seem to separate the individuals better than four groups.

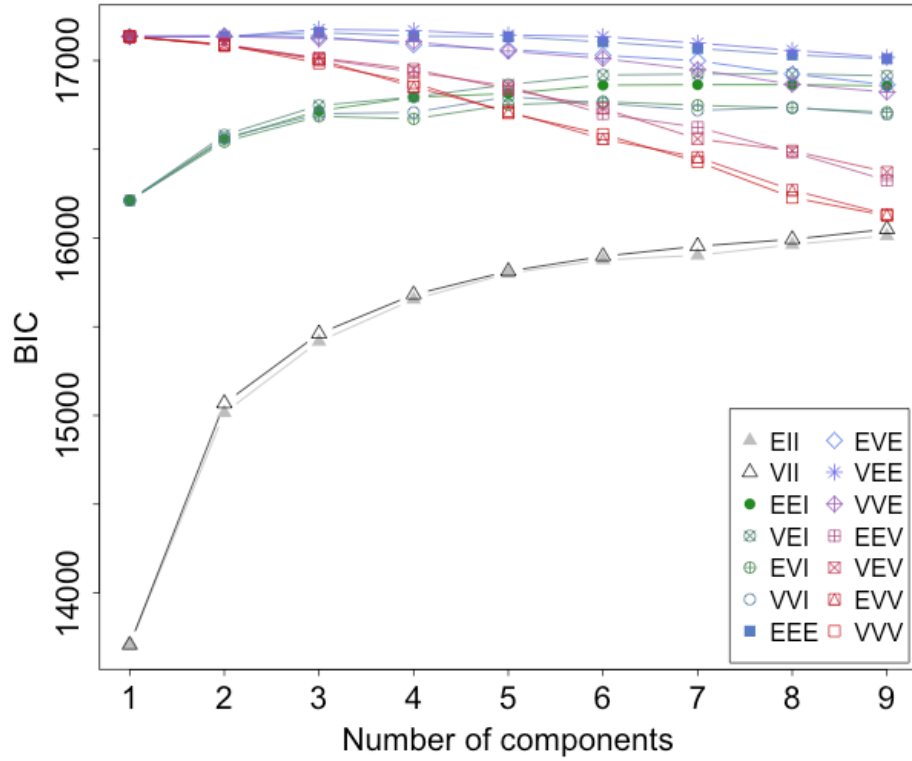


Figure 6. Mclust graph showing the different models and number of components with their corresponding BIC.

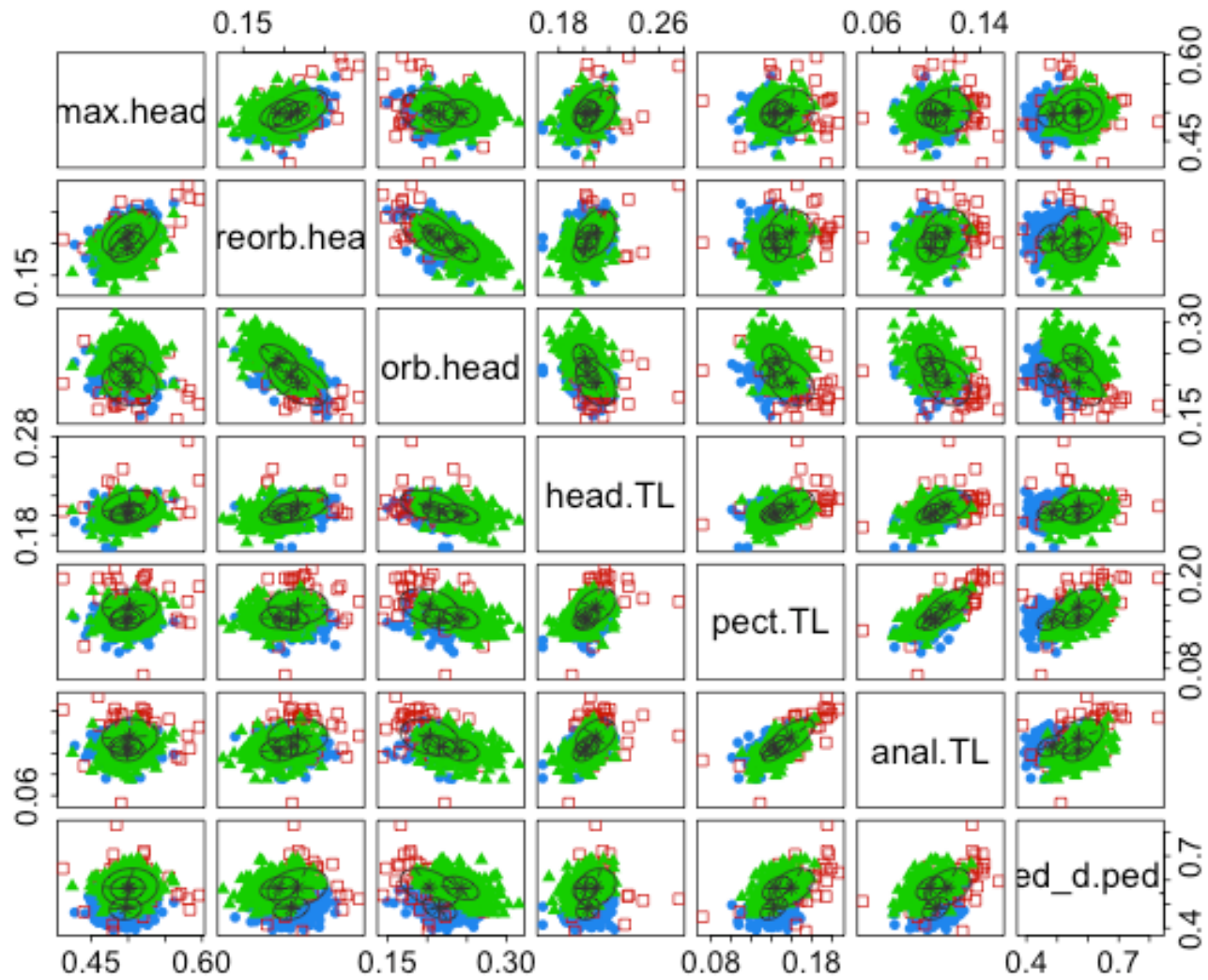


Figure 7. Scatterplot matrix for each bivariate combination of ratios with three groups identified by the Mclust classification shown with different symbols and colors.

The best example for separation using the MClust algorithm (Figure 7) appears to be for the comparison of the orbital/head ratio plotted against the peduncle depth/peduncle length ratio, where there appears to be a fair amount of separation among the three clusters. While there is still substantial overlap present in this plot, the degree of overlap is even greater for the other ratios (Figure 7).

Using three groups with the first two PCs of ratios, Kmeans clustering explained 60.3 percent of the variability, but did not identify distinct groupings, as the majority of the individual data points were within all three groups (Figure 8). Separation among the three clusters is more distinct when using a centroid plot with the first two discriminant functions (Figure 9). The first discriminant function appears to provide the most discriminatory power and is primarily defined by the peduncle depth/peduncle length ratio (Figure 10). Thus, three groups can be fairly well defined by the peduncle depth/peduncle length ratio (Figure 11). However, these clusters do not align with the field-identified morphotypes (Table 2).

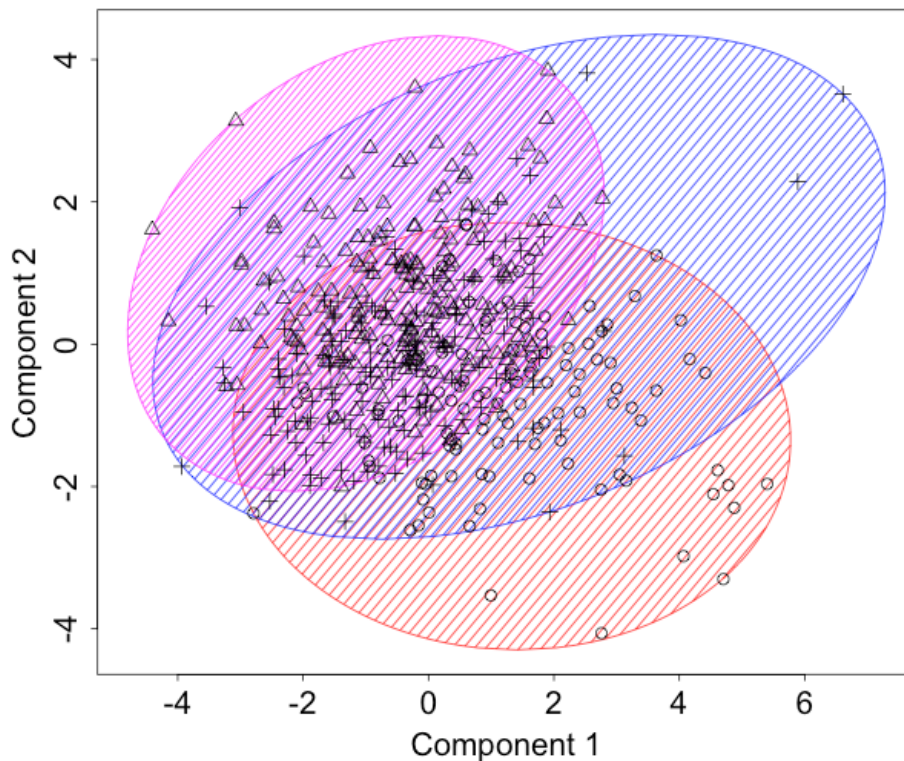


Figure 8. Three Kmeans clusters (different symbols with cluster ellipses of different colors) using the first two principal components of ratios.

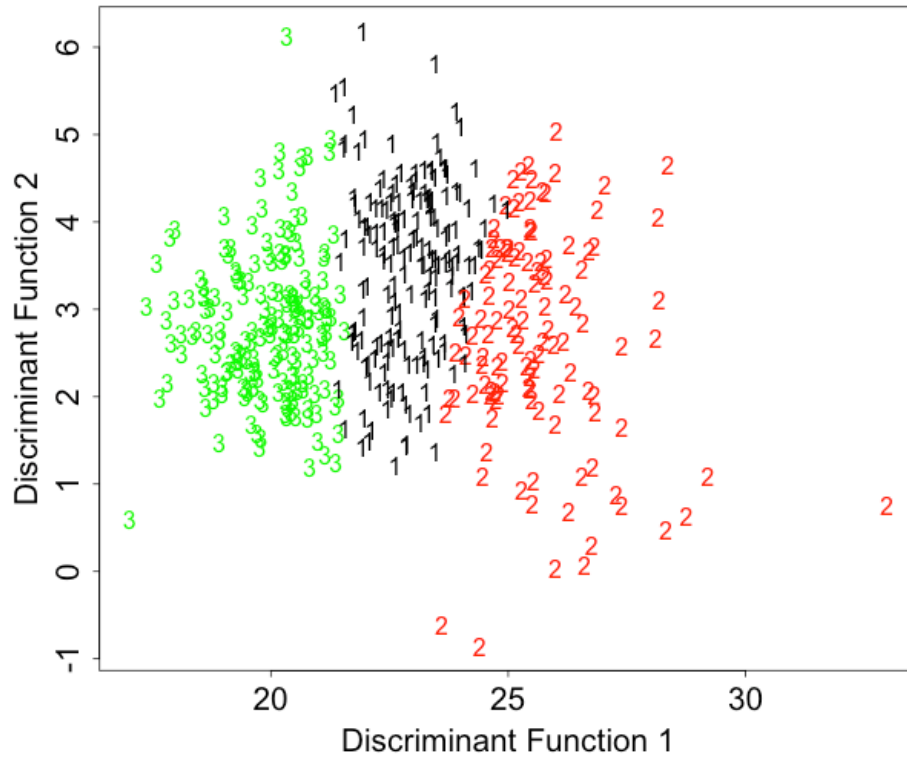


Figure 9. Kmeans centroid plot using the first two discriminant functions of ratios and three groups.

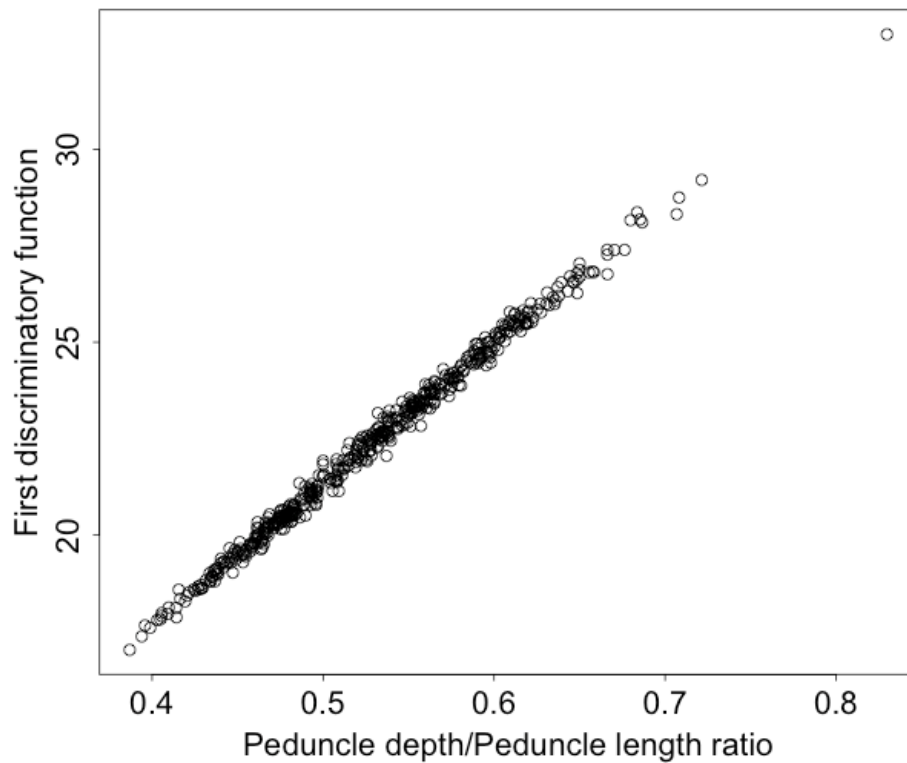


Figure 10. Scatterplot showing correlation between peduncle depth/peduncle length ratio and the first discriminatory function of the Kmeans centroid plot.

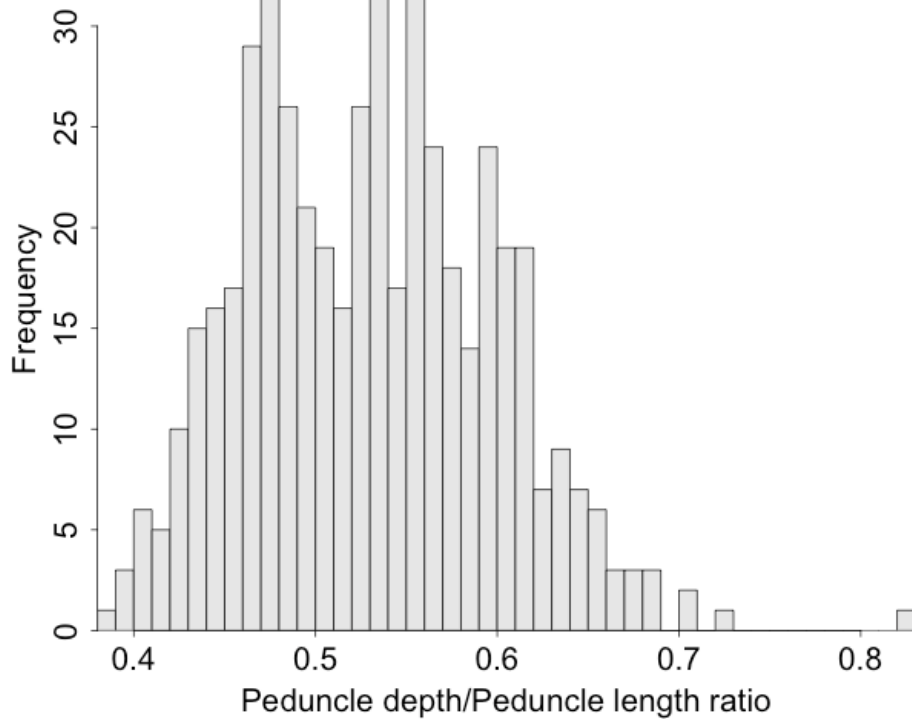


Figure 11. Histogram showing number of individual fish for each peduncle depth/peduncle length ratio.

Table 2. Confusion table with Kmeans cluster ratio groups against field-identified morphotypes.

Field ID	Kmeans Cluster Groups		
	1	2	3
Lean	11	25	26
Humper	33	16	45
Siscowet	118	75	105
Redfin	15	4	11

Discussion

My results show that the current four field-identified morphotypes cannot be predicted from linear combinations of simple ratios of linear measurements. The univariate and bivariate analyses found some slight distinctions, but the multivariate analyses all had overlap and were not very conclusive. Three distinct clusters of individuals were identified with the first principal component that consisted primarily of the ratio of the depth to length of the caudal peduncle. However, these three groups did not closely match the field-identified morphotypes.

The ability to differentiate among field-identified morphotypes may have been difficult for several reasons. First, high variation in the ratios within and low variation in the ratios among morphotypes provided little separation among morphotypes. Second, a predominance of Siscowet Lake Trout in the sample may have negatively affected the DFA as there was a high likelihood of the fish being a Siscowet, regardless of the values of the morphometric ratios. Third, field identification of morphotypes is difficult; thus, the field assigned morphotypes may have been incorrectly assumed to be correct. Finally, sample sizes, especially for presumed Humpback and Redfin Lake Trout, may not have been large enough to fully characterize these morphotypes.

I did, however, find some evidence for separation among individuals in my samples. Kmeans clustering suggested that three distinct clusters might be defined largely by the ratio of the depth to length of the caudal peduncle. While these didn't align with the field-identified morphotypes as suggested above, perhaps that is a sign that there isn't four distinct morphotypes and it works better to cluster the individual fish into three separate morphotypes. Also as the field-identified morphotypes didn't go along with the Kmeans clusters, it could imply that the field-identification is not as accurate and may need to be reconsidered.

Relatively poor distinction between Isle Royale Lake Trout morphotypes in this study contrasts with historical anecdotal accounts that document highly distinct and visually obvious morphotypes in Lake Superior as well as other less disturbed lakes (Rakestraw 1967; Zimmerman *et al.* 2006). A hypothesis as to why there was a lack of discrimination and high variation in this study is that ecological reorganization has occurred. This may be due to long periods of food web change, anthropogenic development, stocking, and fishing exploitation (Muir *et al.* 2014) that has caused a breakdown of reproductive isolating mechanisms that have led to homogenization and reduced differentiation among morphotypes. Fish communities have been altered dramatically, especially native planktivores having been mostly replaced by nonnative ones. This has changed the way energy is transferred through the food web, thus being partially responsible for the reversal in selective forces maintaining diversity among morphotypes (Vonlanthen *et al.* 2012).

There is evidence that Lake Trout diversity in Lake Superior has decreased in the past century: occurrence of well-defined diversity in less perturbed lakes, historical accounts of well-defined diversity before the lakes were disturbed, dramatic declines in Siscowet fat content and changes in population dynamics in the last 50 years, and loss of genetic diversity. Great Slave Lake, Northwest Territories, in northern Canada contains distinct deep and shallow water Lake Trout morphotypes. Great Bear Lake, Northwest Territories, has a lot of diversity, having as many as four well-defined shallow water morphotypes (Blackie *et al.* 2003). Lake Trout from Lake Mistassini, Quebec, can be differentiated using body shape, buoyancy, and body color, as well as life history characteristics (Hansen *et al.* 2012). In all of these examples of morphotype differentiation, morphotypes are easier and more discrete to recognize than the current collections retrieved from Isle Royale. Siscowet Lake Trout sampled during 2009 from Grand Marais, Munising, and Marquette, Lake Superior, had mean percent lipid contents that were very similar to

that of a historical Lean Lake Trout. These changes reflect a shift towards a common resource use, and are expected to increase the ecological variation within and reduce it among morphotypes, making less distinct groups compared to historical populations of Lake Trout (Muir *et al.* 2014). A loss in genetic diversity among Lake Trout in Lake Superior was explained by abundance declines in the 1950's, some local stocks being extirpated, and hatchery stocking of mostly Lean Lake Trout, not a full mix of morphotypes (Guinand *et al.* 2012).

Beginning in the 1800's, the Lake Superior food web underwent dramatic changes, such as the overharvest of Lake Trout and ciscoes (Bronte and Sitar 2008). These changes, as well as invasion by predatory Sea Lamprey and the expansion of nonnative Rainbow Smelt (*Osmerus mordax*), reduced the abundance and diversity of these fishes. All together these have altered the Lake Superior food web and especially Lake Trout diversity.

A century of ecological change altered selection pressures on Lake Trout morphotypes, reducing ecological barriers among morphotypes and allowing them to intermingle and lose their differentiation. It has been demonstrated that at least some of the historical morphological and ecological variation in Lake Superior Lake Trout still exists, but whether this variation and diversity is in a state of ecological release without subsequent reorganization or is headed towards complete breakdown is unknown (Muir *et al.* 2014).

Understanding the diversity in Lake Trout has management implications for conservation and restoration of Lake trout in all the Great Lakes. Historically some of the highest Lake Trout diversity has been reported in waters around Isle Royale (Rakestraw 1967), and restoration of Lake Trout morphotypes at Isle Royale seems to be ongoing. Almost all stocked Lake Trout are of the Lean morphotype, which may not be the best-suited morphotype for some of the habitat they are left in, and this type of habitat only accounts for a small portion of the habitat available in the Great Lakes. Future efforts should be broadened to include other morphotypes in the stocking, with timing and placement consistent with the life history of the particular morphotype. The management of a fishery that holds or targets one morphotype over another will have to consider impacts on the nontarget morphotypes and the processes contributing to the differences among morphotypes (Muir *et al.* 2014).

Although there wasn't much difference found between the morphotypes, there was some evidence of resource polymorphism, or different morphologies within sympatric populations of a species associated with feeding or habitat. Water depth is a primary ecological gradient driving the differentiation of Lake Trout (Eshenroder 2008). In response to differing selection pressures in deep and shallow waters, Lake Trout morphotypes appear to have evolved two ways for buoyancy regulation: hydrodynamic and hydrostatic lift. Lean Lake Trout rely more on hydrodynamic swimming to maintain neutral buoyancy, where as Siscowet and Redfin rely on hydrostatic lift for buoyancy (Webb 1984). These are some more variables that could be added to this model to help better determine differences between the Lake Trout morphotypes around Isle Royale in the future.

There was some hope found in this study, especially with the Kmeans clustering centroid plot, but maybe future studies could build off of this knowledge

with more variables (i.e. habitat type, capture depth) and provide more accurate and better results with further reaching applications.

Acknowledgements

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